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Bulletin

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U. S. DEPARTMENT OF AGRICULTURE.

BUREAU OF PLANT INDUSTRY—BULLETIN NO. 165.

B. T. GALLOWAY, *Chief of Bureau.*

APPLICATION OF SOME OF THE PRINCIPLES OF HEREDITY TO PLANT BREEDING.

BY

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AGRICULTURIST IN CHARGE OF THE OFFICE
OF FARM MANAGEMENT.

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., August 28, 1909.

Sir: I have the honor to transmit herewith and to recommend for publication as Bulletin No. 165 of the series of this Bureau the accompanying manuscript entitled "Application of Some of the Principles of Heredity to Plant Breeding." This paper was prepared by Mr. W. J. Spillman, Agriculturist in Charge of the Office of Farm Management of this Bureau. Great progress has been made during the past ten years in investigations relating to the principles involved in the improvement of plant varieties and the production of new varieties by cross-breeding. Thus far there has been no general statement of the principles applicable in this work especially designed for the use of the actual breeder. The present paper is an attempt to set forth in an orderly manner what is known of the effect of selection on different types of plants and the possibilities of cross-breeding for the purpose of producing new varieties, as understood by the author.

The paper is submitted and recommended for publication in accordance with the fixed policy of this Bureau of giving its men full opportunity of presenting results of scientific and practical interest from different points of view.

The author wishes to acknowledge the helpful criticism of Prof. C. V. Piper, and especially of Assistant Secretary Willet M. Hays, both of whom have carefully read the manuscript and have made many valuable suggestions in the treatment of the various topics.

Respectfully,

B. T. Galloway,
Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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APPLICATION OF SOME OF THE PRINCIPLES OF HEREDITY TO PLANT BREEDING.

INTRODUCTION.

While the discussion in these pages of principles that may be applied in the improvement of crops by breeding and selection will involve principles other than those discovered by Gregor Mendel, the fact that Mendel's principles are somewhat complex renders it necessary to state them in a general way before taking up the subject of plant improvement.

DOMINANCE AND RECESSIVENESS.

The simplest of the principles discovered by Mendel is that which is usually referred to as the "law of dominance." This principle should hardly be called a law, because it is in no wise general and in very few cases is dominance absolute. The phenomena of dominance and recessiveness may be illustrated by a few examples.

If a red-flowered variety of the common garden pea be crossed with a white-flowered variety, the progeny will have red flowers. According to Mendel's original conception a cross of this kind brings together two antagonistic characters. The progeny inherit the red flower color from one parent and the white flower color from the other. It therefore has both these characters. It happens, however, that the red character predominates over the white and comes to expression while the white character is not visible in the cross-bred individual. Mendel suggested that a character behaving as the red character does in this cross should be called a "dominant character," while one behaving as the white character in this cross should be called a "recessive character."

If we cross a bearded variety of wheat with a smooth variety, that is, one that has no beards, the hybrids thus produced either have no beards or the beards will be only slightly developed. Hence, we say that smoothness is dominant to beards, at least partially, or, which means the same thing, that beards are recessive to smoothness. The cross between polled and horned breeds of cattle has no horns, though a small proportion of such cross-bred animals may have "scurs," that is, imperfect horns. Hence, we say that horns are recessive and the poll character dominant. Many other cases might be cited to illustrate dominance and recessiveness of hereditary characters, but the above examples will serve to illustrate the principles sufficiently here.

While it is not uncommon for a character to be dominant or recessive in a cross, it is seldom that dominance is absolute. The presence of the recessive character can usually be detected, and in some cases very easily. Thus, in the cross between bearded and smooth wheat the hybrids usually show a slight tendency to be bearded. Likewise, as already stated, the cross between horned and polled cattle may have scurs. It frequently happens that instead of either of two opposite characters being dominant we get a form intermediate between the two parent forms. Thus, in the cross between ordinary long-headed wheat and the short-headed club wheats of the Pacific coast the hybrid has heads of intermediate length, though they are much more like club wheat than they are like the ordinary kinds, so that the club character is at least partially dominant. In certain crosses between red-flowered and white-flowered ornamental plants the hybrids are pink.

In not a few instances a hybrid is altogether different in some characters from either of its parents. Thus, in the case of the cross between a certain red primrose and a certain nearly related white variety the hybrid is purple.

We thus have every gradation between perfect dominance of a character over its opposite and cases in which the hybrid is unlike either parent.

SEGREGATION.

We have seen that when two naturally opposite characters meet in the same individual one of them may be completely dominant, as the pole character in many individuals of the cross between polled and horned cattle, or the crossbred individual may exhibit a character intermediate between the opposed characters of its parents, as the pink color of certain hybrids between red-flowered and white-flowered plant varieties, or the hybrid may exhibit a character different from the corresponding characters of either of its parents, as the purple color of hybrid primroses produced by crossing certain red and white varieties.

In a pure race of plants having red flowers we may assume that each individual which bears seed transmits to all its seed the tendency to produce red flowers. Likewise, in a pure white-flowered race, each individual transmits to its progeny the tendency to produce white flowers. But what of the hybrid between two such races? What does this hybrid transmit to its offspring? Let us consider the case of the hybrid primrose having purple flowers. The facts are, as found by experiment, that this purple hybrid produces three kinds of progeny. About one-fourth of the seed produced by this hybrid produces plants having red flowers like those of the red-flowered parent of the hybrid. Another fourth have white flowers, while the remaining half have purple flowers. Furthermore, the red and the white flowered plants of this second generation will reproduce only red or white progeny, as the case may be; that is, they behave exactly like pure red or pure white races. On the other hand, every one of the purple-flowered plants will produce in the next generation three kinds of progeny as before. One-fourth of the progeny of these purple-flowered plants will have red flowers, one-fourth of them white flowers, and half of them purple flowers. This experiment was continued by an English florist for fifteen years, always with the same result. The purple always split up into one-fourth red, one-fourth white, and one-half purple, while the reds and the whites thus produced always behaved like pure races of red or white. From these facts we infer that in self-fertilized species an individual which is hybrid with reference to a particular pair of characters tends to produce progeny one-fourth of which is of pure race like one of the parents of the hybrid, another fourth of pure race like the other parent, while the remaining half is hybrid like the original hybrid itself.

Mendel suggested that the cause of these peculiar phenomena is that the hybrid produces two kinds of ovules and two kinds of pollen, the one kind of ovule and one kind of pollen being exactly like those of one of the parents of the hybrid so far as the one character under consideration is concerned, the other kind being like those of the other parent. Let us see how this hypothesis fits the facts.

Suppose the hybrid does produce two kinds of ovules in equal numbers, one of which carries the potentiality of the red flower color, the other that of the white, and two kinds of pollen differing in a similar manner. Let us designate the ovules and pollen carrying red by the letter R, and those carrying white by W. Let us first consider what happens to the ovules of type R. These ovules are offered both R and W pollen in equal quantities. The chances are, therefore, that half the R ovules will be fertilized by R pollen and the other half by W pollen. In the first of these cases, we have R ovules fertilized by R pollen, which would, of course, give pure red individuals. For convenience, we may designate these individuals resulting from the fertilization of R ovules by R pollen as RR individuals. Since half of the ovules produced by the hybrid are supposed to be of type R and since half of these are fertilized by R

pollen it follows that one-fourth of the progeny of the hybrid will be pure reds. Similarly, the *W* ovules are offered both kinds of pollen, and the chances are that half of these ovules, or about half, will be fertilized by *R* pollen, the other half by *W* pollen. The latter half being fertilized by pollen of their own kind result in pure white individuals, which we may, for convenience, designate as *WW* individuals, thus indicating that both the ovules and the pollen which gave rise to these individuals had the character *W*. The *WW* individuals also constitute one-fourth of the progeny of the hybrid. The remaining half of the progeny result from the fertilization of one kind of ovule by the opposite kind of pollen, thus giving hybrids like the original hybrid, which we may designate by the formula *R W*.

We thus see that the supposition that the hybrid produces two kinds of pollen, one like the pollen of the red variety and the other like that of the white, and two kinds of ovules, differing in a similar manner, fully explains the phenomena observed by the breeder of the purple primrose. This hypothesis is further substantiated by the following facts. If we apply the pollen of the hybrid to the stigmas of the red variety, half the progeny thus obtained will be red and half purple. This is easily understood if the hybrid produces two kinds of pollen in equal quantities. All the ovules of the red variety have the character *R*. If half the pollen of the hybrid carries *R*, then half the progeny will be *RR*, or pure red. If the other half of the pollen carries *W*, then the other half of the progeny will be of the type *R W*. That the hybrid produces two kinds of ovules is shown also by the fact that if we apply pollen of the red variety to the stigmas of the hybrid, half the resulting progeny will be red and half purple.

We may accept the hypothesis, therefore, that a hybrid plant whose parents differ in respect to a single character pair produces two kinds of ovules and two kinds of pollen, one kind being like those of one of its parents, the other kind like those of its other parent.

If a hybrid which has in its cells two characters which are naturally the opposite of each other can not produce ovules and pollen with both of these characters in the same ovule or pollen grain, then it follows that these two opposite characters can not be transmitted together. They remain together in the cells of the hybrid well enough, but they fall apart somewhere in the process of producing reproductive cells. Let us now inquire how this segregation of the members of a pair of opposite characters into different ovules and different pollen grains, which takes place in hybrids, may occur. In the cells of a plant we have, first, the outer covering, or cell wall. Within is the nucleus, between which and the cell wall lies the cytoplasm, consisting of a semi-liquid ground substance, in which lies the network of the cytoplasmic reticulum, in the meshes of which occur various small bodies called collectively the cytoplasts. Within the nucleus, which is separated from the cytoplasm by the nuclear membrane, are found the chromosomes, which are small bodies of living substance lying in the nuclear sap or ground substance of the nucleus. We must seek for the potentialities of the hereditary characters either in some of these cell organs or in their relations to each other. The behavior of the chromosomes is such as to suggest strongly that they are the seat of at least some of the potentialities in question. The work of Prof. E. B. Wilson and his pupils and others indicates that in certain animals certain identifiable chromosomes are responsible for the differences between the sexes, at least for the primary sexual differences. Several other hereditary characters not directly related to sex behave in such manner as to indicate clearly that they bear to the chromosomes a relation similar to that which sex bears to these cell organs. It is highly probable, therefore, that many hereditary characters depend in some way not yet understood on the chromosomes. In fact, when we describe the known behavior of the chromosomes we describe the known behavior of Mendelian characters.

It is not necessary in this discussion to consider the various theories regarding the relation of hereditary characters to the organs of the cell. The behavior of the characters studied by Mendel and of hundreds of characters investigated by others leaves no doubt that these characters depend in some way on definite cell organs. This does not necessarily imply that each hereditary peculiarity of a race is represented by a distinct body in the germ cells. A given peculiarity may be due to peculiarities in the composition or the physiological behavior of several cell organs. This much, however, seems to be certain: When two races differ in respect of a character and when the hybrid between these races produces two kinds of reproductive cells, one of which is like the reproductive cells of one of its parents and the other like those of the other parent, as is the case in primroses just cited, then the difference between these two races is due to differences in a single cell organ or to a group of such organs which act together at all times as if they were inseparable. In hybridization we are dealing with differences between organisms, and these differences are due to differences between corresponding cell organs in the different races. For instance, suppose we have two races of plants which differ only in the fact that one of them has red flowers and the other white and that the hybrid between them produces two kinds of pollen, one of which is identical with the pollen of the red variety and the other with that of the white variety. We know that the real difference between these varieties lies in the fact that one of them produces red coloring matter and the other does not. We may therefore assume that in the white variety a certain cell organ fails to perform a function which the corresponding organ in the other variety does perform. We may call this function which is performed in the red variety the "determiner" for red. In the white variety this determiner is absent, although the cell organ which performs this function in the other variety may be present in the white variety. In this variety it fails to perform the function necessary to the production of red coloring matter.

We should not get the idea that red coloring matter is due wholly to a single function of a single body, for such is probably not the case. It may be necessary for several cell bodies to cooperate in the production of this substance. In the white-flowered variety all of these bodies may function properly except one, the failure of the one body to perform its appropriate function being responsible for the nonproduction of the red coloring matter. But when we are dealing with a cross between these two varieties it is the one point in which they differ that concerns us, and we shall use the word "determiner" to apply to this point of difference. Hence, we say that in the one variety the determiner for red is present and in the other it is absent.

Although the determiner of a character is assumed to be a function of a definite body, or of several such, we shall not attempt in what follows to distinguish in all cases between these bodies and their functions. In general, we shall represent the determiner for a character by a capital letter, usually the initial letter of the name of the character. Thus, capital *R* may be taken as the symbol of the determiner for red coloring matter, but this symbol will be used indifferently for the function which produces red and for the body or group of bodies which has this function. For the absence of this determiner in the white variety we shall use the corresponding small letter. Thus, *r* may be considered in what follows as representing the absence of the function *R*, or it may be considered to represent the body present in the white variety that fails to perform the function which is performed by the corresponding body in the red variety.

We are now ready to explain why the hybrid between a red and a white variety of primrose produces two kinds of reproductive cells, one like those of the red variety and one like those of the white—at least, to offer an hypothesis that agrees with the facts.

The red variety has inherited the determiner for red from two parents. The condition of this determiner in the red variety may therefore be represented by the symbol *RR*. This means that in the cells of a plant of the red variety there are two determiners for red. The corresponding determiners in the white variety may be represented by the symbol *rr*, which may be taken as representing two bodies, neither of which performs the function necessary to the production of red coloring matter, but which correspond in the white variety to homologous bodies which do perform this function in the red variety. The symbol of the hybrid would, of course, be *Rr*, in which *R* represents the "active" determiner derived from the red variety and *r* the nonactive one from the white variety. In ordinary growth, when a body cell has attained its maturity and divides into two cells it is supposed that each character determiner present divides, one part going into one of the new cells, the other into the other. Thus, if a mature cell contains the determiners *R* and *r*, then each of the new cells formed by its division likewise contains both *R* and *r*. Thus every cell in the body of the individual may be supposed to have both *R* and *r* in it. This is certainly true of those cells which form the direct line of descent from the original fertilized ovule to the new ovules and pollen grains produced by the individual. The cells in this line of descent are called collectively the germ cells, a term which we shall find convenient to use.

If ovules and pollen cells were formed by ordinary cell division such as that described above, it is clear that every ovule and every pollen grain produced by the hybrid *Rr* would contain both *R* and *r*. But the facts indicate that only half the ovules and half the pollen grains contain *R*, while the other half contain *r*. There must be, then, a cell division somewhere in the line of descent which differs from the ordinary type of cell division, and there is unmistakable cytological evidence that such is the case. Just before the formation of ovules and pollen grains (in fact, in next to the last division of the germ cells) we find a cell division in which the chromosomes do not divide in the usual manner. Instead they unite in pairs, forming double, or bivalent, chromosomes. This union of chromosomes into pairs reduces the number of chromosomes to half what it was before. Then, when the cell divides, these large chromosomes divide, presumably into the two halves which united to form them. If we call the large double chromosomes mother chromosomes and the small ones into which they separate daughter chromosomes, then in this cell division one of the daughter chromosomes passes to one of the newly formed cells, while the other passes to the other cell. Now, if these chromosomes either themselves are the bodies whose functions are our "determiners," or if they contain smaller bodies which are responsible for the determiners, we have at once an explanation of the fact that our hybrid produces two kinds of ovules and two kinds of pollen. For in this cell division, which is called the reduction division because in it the number of chromosomes is reduced by half, our determiners *R* and *r* may be assumed to reside in separate chromosomes which unite to form a single bivalent. While cell division is taking place this bivalent chromosome again separates, *R* passing into one daughter cell and *r* into the other. If the determiners *R* and *r* are not simply the functions of chromosomes themselves they at least pertain to bodies which at some point in the line of descent of the germ cells behave just as we know the chromosomes do behave—that is, at some cell division *R* and *r* unite into a pair, and when division occurs *R* goes one way and *r* the other. Two determiners which thus behave toward each other are said to constitute a Mendelian pair.

Most Mendelian pairs consist simply of the presence of a given determiner on the one hand and the absence of that determiner on the other. Furthermore, the determiner which represents the presence of a character is in nearly all cases dominant over the determiner which represents the absence of that character. Dr. C. B. Davenport, of the station for experimental evolution of the Carnegie Institution, found that in poultry practically all the character pairs known show this relation; i. e., presence of a character dominant and absence of it recessive. We have seen, however, that there are some exceptions to this rule, since the poll character is dominant to horns and beardlessness in wheats is dominant to beards. The difference between polled and horned cattle is the absence of horns in one and their presence in the other.

But cases are known in which this simple relation of presence and absence of a character does not constitute the Mendelian pair. For instance, if Barred Plymouth Rock females be mated with Indian Game males all the female progeny of this mating will be black, while all the males will be barred like the mother. Data accumulated by the writer and an extended series of experiments performed by Mr. H. D. Goodale[a] indicate that the female Barred Plymouth Rock produces two kinds of eggs. One of these kinds is destined to produce females, and these female-producing eggs do not have the determiner for barring in them. The other kind is destined to produce males, and these eggs do have the barring factor. In this case it appears, therefore, that the determiner for femaleness and that for barring form a Mendelian pair. Wilson has apparently shown that the determiner for femaleness in many animals is a certain chromosome or group of chromosomes that always act as a unit. If we assume that the determiner for barring is another chromosome which unites with the sex element to form a bivalent in the reduction division we have at once an explanation of the behavior of the determiner for barring. In the germ cells of the female Barred Plymouth Rock we have the two elements *F*, which causes the individual to be a female, and *B*, which gives the barring on the feathers. In ordinary cell division both of these elements divide; but in the reduction division *F* and *B* unite into one body. This body then separates as the cell divides, so that one of the daughter cells contains *F* and the other *B*. Such a female therefore produces two kinds of eggs, one containing the determiner for the female sex, the other that for barred feathers.

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[a] See Science, June 25, 1909.

Several other cases are known in which Mendelian pairs are formed of determiners for characters that are apparently unrelated. Such a case occurs in the purple primrose previously mentioned. We may explain the phenomena presented by this hybrid as follows: Let us assume that the original wild species from which the red and the white races in question are descended had purple flowers and that this purple color was due to two functions of the same cell organ. One of these functions, which we may designate as *R*, had to do with the production of red coloring matter, while the other, which we may designate as *P*, changed red into purple, somewhat after the manner in which an alkali changes litmus from red to blue.[a] The determiners *R* and *P* were functions of the same cell organ, probably a chromosome. Since this body had two functions we may represent it by the symbol *R–P*, the hyphen indicating that the two functions belong to the same cell organ. Since there is a pair of these bodies in each cell, the complete status of these determiners in the body cells would be represented by *R–P R–P*.

Now, let us suppose that in one section of the species the determiner *R* becomes latent or is lost. Our formula then becomes *r–P r–P*, or simply *PP* in this race, which would, of course, have white flowers, since the determiner for red is absent. In another section of the species the determiner *P* vanishes, leaving *R–p R–p* or simply *RR*. Now, when we cross these two races we bring the determiner *r–P* into the same cell with *R–p*. Here we have the red coloring matter produced by one determiner and converted into purple by the other. This would account for the purple color of the hybrid, as well as the red of one variety and the white of the other. Other cases of Mendelian pairs of this nature will be mentioned later.

In this purple hybrid we may consider that we have one character pair consisting of *R* from the red parent and *r* from the white parent, so that this pair consists of red and absence of red, while along with it we have another pair consisting of *P* from the white parent and *p* from the red parent, so that this pair consists of the presence of *P* and the absence of *P*. But the fact that *P* and *R* can not be transmitted together indicates that *R* and *p* pertain to the same cell organ, and that *r* and *P* pertain to the Mendelian mate of this organ. Since most Mendelian character pairs consist of determiners one of which represents the presence of something and the other the absence of the same thing, we shall, in general, use for such pairs of characters in hybrids symbols consisting of a capital letter and the corresponding small letter, the capital letter standing for presence of the character and the small letter for its absence. Thus, in the cross between red and white peas, since the difference between these varieties consists in the presence of red color in one and its absence in the other, we represent the hybrid as *Rr*. Since the hybrid itself is red in this instance, this formula is logical; it would naturally be red because of the presence of *R*. But, as previously stated, there are cases in which the absence of a character is dominant in the hybrid between races one of which has the character and the other does not. Thus the hybrid between polled and horned cattle is polled. Here the formula for the horn determiner in the pure horned breed would be *HH;* in the pure polled breed, *hh;* and in the hybrid, *Hh*. But since the determiner *H* does not succeed in producing horns in the hybrid and the hybrid therefore has the appearance of its polled parent we may write the formula for the hybrid as (*H*)*h*, to show these facts. Similarly, the hybrid between bearded and smooth wheat would be represented by (*B*)*b*.

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[a] See article by Shull in American Naturalist, July, 1909.

Cases like the purple hybrid primrose are so rare that we do not need to use any particular symbol to indicate that the hybrid is unlike either parent.

The question why these characters, horns in cattle and beards in wheat, do not develop when represented by only one active determiner is an interesting one, and is very ably discussed by Doctor Shull in the July, 1909, number of the American Naturalist. The fact probably is that in these hybrids the determiners *H* and *B* are not latent, but that single determiners are not able to produce that chemical condition in the cell which is necessary for the development of these characters. In pure horned cattle and pure bearded wheat, where there are two active determiners for each of these characters, the proper condition for the development of these characters is brought about.

In general, a hybrid produces three types of progeny with reference to each pair of characters in which its parents differ. The hybrid between red and white varieties of peas produces two kinds of pollen, which we may designate as *R* pollen and *r* pollen. It produces two corresponding types of ovules. On the average, half the *R* ovules are fertilized by *R* pollen, so that one-fourth of the progeny of such a hybrid is of the type *RR* or pure red. Likewise, half the *r* ovules are fertilized by *r* pollen, giving *rr* individuals, which constitute one-fourth of the second generation. The remaining half of the *R* ovules meet *r* pollen and the remaining half of the *r* ovules meet *R* pollen, giving in each instance the combination *Rr*, which constitutes half the second generation. If *R* is completely dominant the types *RR* and *Rr* can not be distinguished, since the latter has red flowers like those of type *RR*. Hence, where dominance is complete the second generation appears to consist of only two types. One of these types shows the dominant character, the other the recessive character, and the dominant type is three times as numerous as the recessive. Thus we arrive at the well-known Mendelian ratio of 3:1, or three dominants to one recessive in the second generation of a hybrid.

In the above second generation the two types *RR* and *rr* are seen to consist of like things united, while the type *Rr* consists of unlike things united. Types *RR* and *rr* are said to be homozygote, a term which means "like things united," while *Rr* is said to be heterozygote, which means "unlike things united." An individual is said to be homozygote with reference to a given character when the cells of that individual contain two determiners for the presence of that character. If its cells contain only one determiner for any character it is said to be heterozygote for that character. Thus a bearded wheat is homozygote for beards, a pure race of smooth wheat is homozygote for absence of beards, while a cross between a bearded and a smooth race is heterozygote for beards.

ALLELOMORPHISM.

The term "allelomorph" was introduced by Prof. William Bateson, of Cambridge, England, one of the leading investigators of Mendelian phenomena. It is derived from two Greek words, one of which means "one another" and the other "form." We may say that it means "corresponding forms." What we have called a "pair of determiners" Bateson calls a "pair of allelomorphs." The term "allelomorph," however, has a wider application than "determiner;" it may mean characters themselves as well as the determiners of those characters. To say that one character is allelomorphic to another means simply that the two characters when brought together in the same individual form a Mendelian pair and hence fall apart when reproductive cells are produced. Thus, a pair of allelomorphs is what we have been calling a "pair of Mendelian characters." Hence, the term "allelomorph" is frequently used simply to mean a Mendelian character; that is, a character which obeys Mendel's law of segregating from its mate in the reduction division.

The term "gamete" is also a very convenient one which we shall have occasion to use frequently. It simply means a reproductive cell, such as an ovule, a pollen grain, an unfertilized egg, etc.

LAW OF RECOMBINATION.

The third and most important principle discovered by Mendel[a] is the fact that, generally speaking, when two or more "pairs" of characters are present in the same hybrid these pairs are independent of each other, so that one member of a given pair may be transmitted with either member of another pair. The results of this important discovery are shown in Table I, which illustrates the cross between Polled Durham and Hereford cattle.

As is well known, Polled Durham cattle have colored faces and no horns, while Herefords have horns and white faces. The white face of the Hereford seems to be due to the presence of a determiner which controls the distribution of color over the body. We thus represent white face by W and colored face by w, that is, absence of white face. As before, the poll character is represented by h and the horn character by H. White face is dominant to colored face in this cross. The complete formulæ for these two pairs of characters in the body cells are, therefore—

In pure Hereford cattle, $HHWW$.
In Polled Durham cattle, $hhww$.
In the cross, $(H)hWw$.

The cross has the white face but no visible horns, though it may have scurs.

The squares in the upper part of Table I represent germ mother cells dividing in the reduction division. In this division each pair of characters is separated. Thus, the pair Hh, both members of which have been present in every cell of the body of the hybrid, is here separated, H going to one daughter cell and h to the other. In the cross here under consideration we have a second pair of allelomorphs, namely, Ww. When a given mother cell divides, the two pairs of allelomorphs may be arranged as in the left-hand square at the top of Table I, in which case H and w go together into one daughter cell, while h and W go into the other. Such a division gives two kinds of gametes, the formulæ for which are, respectively, Hw and hW.[b] Or the two pairs of allelomorphs may be arranged as in the right-hand square of Table I, in which case H and W go to the same daughter cell, while h and w go to the other, giving two kinds of gametes having the respective formulæ HW and hw. There are, in all, therefore, four kinds of gametes that a hybrid individual of the type here under consideration can produce, namely, *Hw*, *h W*, *H W*, and *hw*. In the first of these four types of gametes, namely, *Hw*, we find horns being transmitted with colored face; in the third, *H W*, horns and white face are transmitted together. Likewise, in the second type, *h W*, we have the poll character and white face together, while in type four, *hw*, we have the poll character and colored face.

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[a] The first is the so-called "law of dominance," though it is hardly entitled to rank as a law; the second is the law of segregation of character pairs.

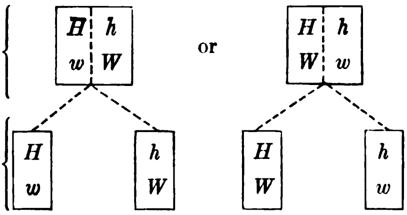
[b] The gametic formula Hw does not represent a pair of determiners. It represents two determiners, one of which is from one pair and the other from another pair. We do not have pairs of determiners in gametes, i. e., in reproductive cells. The pairs separate in the reduction division, and a gamete never has both members of the same pair.

Since in the reduction division either of the two possible arrangements of the two pairs of allelomorphs is just as likely to occur as the other, one of them will occur in about half the cells and the other in the other half. We thus get all four types of gametes in equal numbers in every hybrid animal of this character. In the male this is actually realized, for millions of gametes are produced. But in the female only a few reproductive cells are formed, but these few are as likely to be of one type as another. Hence, on the average for a large number of such females, the four types of gametes will occur equally often. In the middle part of Table I we have all the possible, and equally probable, unions that can occur between the gametes of the two sexes. Thus the *Hw* gametes of the female are offered four kinds of sperm in equal numbers. Hence, on the average one-fourth of these *Hw* ovules will be fertilized by *Hw* sperm, giving individuals of the next generation of the type *HHww*. Another fourth will meet *h W* sperm, giving individuals of the type *(H)h Ww*, and so on.

TABLE I.—*Cross between Polled Durham and Hereford cattle and its results.*

Reduction division as it occurs in the cells of the first-generation hybrid.

The four types of reproductive cells produced by first-generation hybrids.



Or simply *Hw*, *hW*, *HW*, *hw*.

The sixteen possible, and equally probable, matings to produce second-generation hybrids are as follows:

Gametes of male.

Gametes of female.	*Hw*	*hW*	*HW*	*hw*
Hw	1 *HHww*	2 *(H) hWw*	3 *HHWw*	4 *(H) hww*
hW	5 *(H) hWw*	6 *hhWW*	7 *(H) hWW*	8 *hhWw*
HW	9 *HHWw*	10 *(H) hWW*	11 *HHWW*	12 *(H) hWw*
hw	13 *(H) hww*	14 *hhWw*	15 *(H) hWw*	16 *hhww*

The nine different combinations and their relative frequency follow:

1 *HHWW*.	2 (*H*) *hWW*.	1 *hhWW*.
2 *HHWw*.	4 (*H*) *hWw*.	2 *hhWw*.
1 *HHww*.	2 (*H*) *hww*.	1 *hhww*.

The sixteen formulæ in the squares in the middle of Table I show the results of these sixteen unions. It will be seen that some of these matings are alike; for instance, 2, 5, 12, and 15; 3 and 9; 4 and 13. There are only nine different kinds, as shown in the lower part of Table I. These nine different combinations occur in the relative frequencies shown in the numbers preceding each of the nine in the lower part of Table I. Thus, one-sixteenth of the progeny will represent the combination *HHWW*, four-sixteenths the combination (*H*)*h Ww*, and so on.

Table II shows the results of a more complex cross which the writer made while connected with the Washington Agricultural Experiment Station, Pullman, Wash. It is a cross between two varieties of wheat, one of which was a winter wheat that lodged easily (that is, had weak straw) and had open chaff, and thus when ripe shattered its grain easily. The other was a variety of spring wheat that did not lodge and had tightly closed chaff when ripe. The first generation[a] of the hybrid inherited a very complex lot of characters. Thus, it inherited both winter and spring character; both the lodging and the nonlodging tendency; both the open and the closed chaff tendency. In this cross the winter character, the nonlodging tendency, and the closed-chaff tendency were dominant. Letting—

W stand for the winter character,
w for absence of winter character (i. e., spring character),
N for nonlodging (i. e., for stiff straw),
n for absence of *N* (i. e., for weak straw),
C for closed chaff, and
c for absence of *C* (i. e., for open chaff),

the formula of the hybrid was *WwNnCc*. Now this hybrid can produce, and does produce, in about equal numbers eight different types of ovules and eight similar types of pollen, namely, *WNC*, *WNc*, *WnC*, *Wnc*, *wNC*, *wNc*, *wnC*, *wnc*. The union of these eight types of ovules and pollen grains gives sixty-four possible, and equally probable, matings. But, as before, some of these matings give identical results; for instance, *WNc* × *WnC* and *WNC* × *Wnc* both give *WWNnCc*. There are, however, twenty-seven different combinations amongst the sixty-four matings; these, together with the number of matings in which each occurs, are shown in Table II.

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[a] Professor Bateson uses the symbol F_1 for first-generation hybrids. The F is the initial letter of the word "filial." Hence this symbol means "first filial generation." Bateson denotes the second and later generations of a hybrid by F_2, F_3, etc. Likewise, he denotes parental generations as follows:

P_1=parents of the hybrid.
P_2=grandparents of the hybrid.
P_3=great-grandparents, etc.

TABLE II.—*The twenty-seven different types in the second generation of a hybrid between a winter wheat, W, with weak straw, n (absence of nonlodging character), and open chaff, c (absence of closed chaff), and a spring wheat, w (absence of winter character), with stiff straw, N (nonlodging), and closed chaff, C.*

Serial No.	Proportions.	Formulæ of the types.	Serial No.	Proportions.	Formulæ of the types.	Serial No.	Proportions.	Formulæ of the types.
1	1	*WWNNCC*	10	2	*WwNNCC*	19	1	*wwNNCC*
2	2	*WWNNCc*	11	4	*WwNNCc*	20	2	*wwNNCc*
3	1	*WWNNcc*	12	2	*WwNNcc*	21	1	*wwNNcc*
4	2	*WWNnCC*	13	4	*WwNnCC*	22	2	*wwNnCC*
5	4	*WWNnCc*	14	8	*WwNnCc*	23	4	*wwNnCc*
6	2	*WWNncc*	15	4	*WwNncc*	24	2	*wwNncc*
7	1	*WWnnCC*	16	2	*WwnnCC*	25	1	*wwnnCC*
8	2	*WWnnCc*	17	4	*WwnnCc*	26	2	*wwnnCc*
9	1	*WWnncc*	18	2	*Wwnncc*	27	1	*wwnncc*
	16			32			16	

16+32+16=64.

Types Nos. 1, 3, 7, 9, 19, 21, 25, and 27 are homozygote, and will all reproduce true to seed. Type No. 1 was the type sought in this cross.

The first nine of these twenty-seven types, constituting one-fourth of the whole generation, are pure winter wheat (*WW*), the next nine (Nos. 10–18), constituting one-half of the generation, are hybrids between winter and spring (*Ww*), while the last nine, constituting one-fourth, are pure spring wheats (*ww*). Each of these three groups of nine types is subdivided in like manner into one-fourth pure nonlodging, one-half hybrid between lodging and nonlodging, and one-fourth pure lodging. Thus, the first three types are all pure winter and pure nonlodging; these three types constitute 4 sixty-fourths of the generation, or one-fourth of the first group of nine. The second group of three are all pure winter, but hybrid with reference to the lodging character; these three constitute 8 sixty-fourths of the generation, or one-half of the first group of nine, etc. Thus, each of the three groups based on the winter-spring character pair is subdivided into three groups based on the straw character, thus giving nine groups based on these two character pairs. Each of these nine is similarly divided into three types, based on chaff character. This gives in all twenty-seven different combinations. Of these twenty-seven combinations, eight are seen to be homozygote with reference to all three character pairs. This means that these eight are pure bred as far as these characters are concerned and will show these characters in all their progeny. The other nineteen types are heterozygote, or cross-bred, with reference to one or more of the character pairs, and will thus not reproduce true to seed.

The one combination which was sought in this cross is type No. 1 of Table II. This type constituted only 1 sixty-fourth of the second generation of this hybrid. It is the combination *WWNNCC*, which is pure winter wheat, nonlodging, with tightly closed chaff. The most undesirable type, *wwnncc*, also occurred once in sixty-four times—that is, it was a spring wheat which lodged and had weak chaff. Further mention of this new type of wheat will be made later in discussing the application of the principles to plant breeding.

We may now state the law of recombination as follows: In the second generation of a hybrid there tends to occur every possible combination of the original parent characters.[a]

We may further add to this law that every one of these combinations will, if the second generation is numerous enough, occur in some individuals in homozygote form, and will thus be firmly fixed and reproduce true to seed.

Although all the possible combinations will occur in the second generation of a hybrid (that is, provided the second generation is numerous enough to permit them to occur) unfortunately most of them will be mixed with other combinations that have the same external appearance but very different hereditary tendencies. This is due to the fact of dominance. For instance, the homozygote form *WWNNCC* of Table II can not be told by inspection from the form just following it (*WWNNCc*) or from several other of the twenty-seven combinations. One way to overcome this difficulty in a self-pollinated species is to save the seed of each second-generation plant separately. If the species is one that is not self-fertilized, but one which can be artificially self-fertilized, we can accomplish the segregation of the desired type by artificial self-fertilization of all the second-generation individuals that appear to be of the type desired and by planting their seed separately. When the next generation matures it will be seen which of them have reproduced true to type. The seed of these may be saved, and thus form the basis of a new and fixed variety in self-fertilized species and in such open-fertilized species as will endure such self-fertilization.

A very beautiful illustration of the law of recombination is seen in the work of Professors Price and Drinkard, of the Virginia Agricultural Experiment Station, in their experiments with hybrid tomatoes. Two varieties were crossed which differed in three respects, namely, one variety had green leaves, the other yellowish green; one had red fruit, the other yellow; one had pear-shaped fruit, the other round.

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[a] The writer discovered this law independently in 1901. See Bulletin No. 115, Office of Experiment Stations, U. S. Dept. of Agriculture.

In the second generation of this hybrid every one of the eight possible combinations of these three pairs of characters was found, as follows:

Serial No.	Leaf color.	Fruit color.	Fruit shape.
1	Green	Yellow	Round.
2	Green	Yellow	Pear-shaped.
3	Green	Red	Round.
4	Green	Red	Pear-shaped.
5	Yellowish	Yellow	Round.
6	Yellowish	Yellow	Pear-shaped.
7	Yellowish	Red	Round.
8	Yellowish	Red	Pear-shaped.

Two of these eight types were like the original parent varieties, the other six were new. This case illustrates well the power a knowledge of the law of recombination puts into the hand of the breeder. Breeders have unconsciously used this law since breeding first became an art, but a knowledge of the principles involved now enables them to accomplish desired results much more quickly and surely than was formerly the case.

FLUCTUATING VARIATIONS.

From what has been said concerning the law of recombination it is easy to see that in a species which naturally cross-fertilizes in the field we are continually getting new combinations of hereditary characters. For instance, in a cornfield hardly any two plants can be found that carry exactly the same combination of hereditary characters. If we should take a single grain of corn and plant it where it can not cross-fertilize with another its progeny would break up into types somewhat as shown in Table II, except that, instead of stopping with twenty-seven different types, each of these would be subdivided into three others, and each of these again subdivided in the same way, and so on within the limits of the number of separate and independent hereditary characters for which the grain we started with was heterozygote. Generally speaking, only a comparatively few of these characters will be important to the breeder, so that the others may be neglected. But we must not overlook the fact that in the main the remarkable fluctuations of characters seen in a cornfield are due to this recombination of characters from year to year. On the other hand, if we take a single grain of wheat and plant it, then save every seed of it for planting, the plants produced in the second generation would, ordinarily, be exactly alike in so far as their combinations of hereditary characters are concerned. This is because under ordinary field conditions wheat is self-fertilized, and a field of wheat in the main consists of plants that are completely homozygote with reference to every one of their hereditary characters. When we do get a plant which is completely homozygote in all its characters, then it will transmit the same form of every character to all its offspring, and we have eliminated all variations due to recombination of characters. There will still be differences between the plants grown from the same seed, but these differences will be due to environmental influences, such as differences in available moisture, plant food, sunlight, and the like. It is highly important to make this distinction between individual variations which are due wholly to environment and those which are due to recombinations of hereditary characters. It will be seen later that so far as experimental evidence goes there is much reason to believe that selection of those fluctuations which are due wholly to environment as a rule has no effect whatever in changing the hereditary characters of the plant. On the other hand, in those plants which are not homozygote in all their characters, as is practically always the case in a species that regularly cross-fertilizes, there will be variations due to recombinations of different characters, and selection will have a marked effect in species of this kind. The effect of selection on fluctuating variations has been much confused because of the effect produced by mass selection in mixed populations of fixed forms like wheat, which effect will be further discussed later. In wheat, and other self-fertilized species, individual selection—that is, selection in which we keep the progeny of each mother plant separate—soon proves that we can not modify these fixed strains by selection; that is, generally speaking. The facts have further been confused because of the effect which either mass or individual selection has in gradually changing the character of cross-fertilized crops like corn. In these cross-fertilized crops either mass selection or selection annually to a single mother plant causes a gradual change in the direction of the selection. But when we eliminate the effect of the law of recombination, which occurs continually in cross-fertilized forms, and practice selection annually to a single mother plant, we find that it is apparently impossible to produce modification by selection, except in rare instances. The investigations on which this reasoning is based will be given later in these pages.

The amount of investigation which this subject has received can hardly be said to be sufficient to settle it for all cases, for there are a few exceptional cases which do not behave in the usual way and which are not understood. In the main, however, the investigations all agree. The first work bearing strictly on the effect of selection on forms from which all variation other than fluctuating variation due to environment has been eliminated was done by Prof. W. Johannsen, of Copenhagen, on beans and barley. This work will be referred to more in detail when we come to consider the effect of selection on self-fertilized species, as will also the remarkably accurate work of Doctor Nilsson, whose work at Svalöf, Sweden, is so well known through the writings of De Vries. Some of the work on vegetatively propagated species will be given in dealing with the effect of selection on this class of plants.

RUNNING OUT OF VARIETIES.

It is quite generally believed that there is a tendency for vegetatively propagated varieties to "run out." This subject has received much discussion but very little careful investigation. There is no question that in many species such varieties do lose vigor and become practically worthless after a few years. Carnation growers all agree that varieties of these plants are short lived. Varieties of carnations seldom retain their vigor a dozen years. It is generally believed that varieties of potatoes retain full vigor only for a few decades. With no selection this is undoubtedly true. We do not know just what effect careful selection to maintain yield might have on the length of life of a variety of potatoes. It is certain, however, that the old Peachblow potato, so popular half a century ago, has been maintained in full vigor by selection to the present time. Mr. E. H. Grubb, of Colorado, one of the leading potato growers of that State, is now growing this variety and finds it an excellent yielder. It is probable, however, that potato varieties do tend to run out. The same may be said of apples, but, as in the case of potatoes, definite investigations on this point are lacking.

On the other hand, there are species that have completely lost the power of producing seed, as, for example, the banana. These have been propagated vegetatively for ages without loss of vigor. But we can not say that the same variety persists indefinitely, because the facts are wanting. It is probable that among vegetatively propagated races we may find every gradation between races which run out very quickly and those which remain vigorous indefinitely.

A good many species of plants produce seeds parthenogenetically,[a] as the dandelion, certain species of Hieraceum, etc. These are among our most vigorous weeds. How long they have propagated asexually we do not know. They may, however, be cited as instances of plants which apparently retain their vigor through long periods without recourse to sexual propagation.

What has been said of races propagated vegetatively applies equally to those which are habitually self-fertilized, with perhaps the difference that in most such species there may occasionally occur cases of cross-fertilization. It is quite generally assumed that self-fertilized races tend to run out. There is some evidence that such is the case. This is especially true of varieties of wheat. A single variety seldom retains its supremacy in any given locality for half a century. Yet it is far from demonstrated that careful selection of wheat varieties would not maintain vigor almost indefinitely. This whole question of the running out of varieties needs much further study before the last word can be said on the subject.

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[a] That is, without fertilization. In these plants the reduction division is omitted in those mother cells which develop into seeds.

Having outlined the main principles with which we have to deal in plant breeding, we may now proceed to a consideration of the different methods of breeding and selection and the application of the principles involved.

SELECTION WITHOUT ARTIFICIAL CROSSING.

We have already seen that close-fertilized and cross-fertilized species behave differently under selection. In addition to self-fertilized and cross-fertilized species we must also consider the effect of selection on those varieties which are propagated vegetatively; that is, from cuttings, grafts, tubers, etc., including all methods of propagation other than from seed.

VEGETATIVE PROPAGATION.

In plants propagated vegetatively we have several kinds of variation to consider, for the effect of selection on each of these is different. First, we have those fluctuating variations which are due wholly to environment, such as difference of food supply, moisture conditions, etc., which modify the individuals of a generation but which are not hereditary. As we have already seen, such investigations as have been made on this subject indicate that in nearly all cases of fluctuating variation due to environment selection is entirely without permanent effect in changing the plant from year to year. In Bulletin No. 127 of the Illinois Agricultural Experiment Station Dr. E. M. East made a careful survey of all the literature he could find relating to the effect of selection on these fluctuating variations in potatoes. He concluded that it is not proved that selection can change these variations, though the question is left in some doubt.

Prof. H. S. Jennings, of Johns Hopkins University, has during the past few years made some investigations on the unicellular animal Paramecium which must rank among the most important biological work that has been done, at least in the field of experimental evolution. While Paramecium is an animal, it propagates for hundreds of generations by simple division, and hence there is every reason to suppose that the principles applicable to Paramecium are applicable to plants which are propagated vegetatively. Jennings gives an excellent summary of his work in the American Naturalist for June, 1909, where reference will be found to the original technical publications. First, he studied abnormal individuals to see whether or not their abnormalities were inherited. In many of his cultures individuals could be found that had various peculiarities. Although he sought patiently for some peculiarity of this kind that might be inherited and although he found many such peculiarities, in no case did he find one that is inherited in the proper sense of the word. The peculiarities in question never appeared in both of the individuals resulting from a division. Thus there was no tendency for them to multiply and spread over the race. Concluding his discussion of such cases, Jennings remarks: "Examination of a large number of cases in Paramecium shows that these untypical characters are never reproduced in the young."

Jennings also found that the descendants of a single individual varied greatly in size. This suggested the idea that by selecting continually from the largest and the smallest, two races could be developed which would differ in size, although descended from the same original individual. This experiment was carried on for a very long series of generations, one line consisting of the largest individuals that could be found and of their largest progeny, the other of the smallest individuals and their smallest progeny. At the end of the experiment the two lines were brought under the same environmental conditions and within a very short time the average length of the two types became identical. This led Professor Jennings to remark that "Selection within a pure race is of no effect on size," and again, "Neither selection nor environmental action changes the size of the pure race."

This investigator found eight distinct types of Paramecium in a group which was previously supposed to consist of two species differing in size. Figure 1 illustrates the relative sizes of the individuals in these eight races. It is seen that even the extreme forms overlap, and it was found that if the smallest individual of the largest race be selected and its progeny grown with continual selection from the smallest individuals to be found, no matter how long such selection was continued the progeny of this small individual would soon cover the whole gamut of variation of the race to which it belonged, and the same was true for each of the other races. Speaking of the effect of selection on such a species, Jennings says:

> How will selection act on such a complex species? As we have seen, selection within a single race is without effect. But if we make selections among the individuals of a mixed collection of races, such as figure 1 shows, we reach most instructive results. By making our selections in the proper way, we for a time make steady progress toward a certain goal. We will suppose that we do not know of the existence of these races; this is the case with most experiments in selection. From the species as a whole, as shown in figure 1, we will select for increased size. Let us follow the old plan of selecting many individuals showing the desired character; we will preserve all specimens above the mean size of the entire collection; that is, we divide the

collection at x—x, rejecting all those to the right. By so doing it is evident that we exclude all specimens of the two smallest races *c* and *i*, while preserving the majority of the specimens of the larger races. Allowing these to propagate, we of course get a mixture of the remaining larger races. Hence the mean size of the whole collection will be greater than at first. Selecting again those above the mean size of this lot, we drop out another small race, and the mean of the collection as a whole again rises a little. We are making good progress in the improvement of our species. By taking successive steps of this character, dropping out the smaller races, first partly, then completely, one after another, we can for a long time continue to improve by selection, but finally we reach a stage in which all but the largest race have been excluded. Thereafter we can make no further progress. In vain we choose for breeding the largest specimens of the lot; all belong to the same race, so that all produce the same progeny. Selection has come to the end of its action. * * *

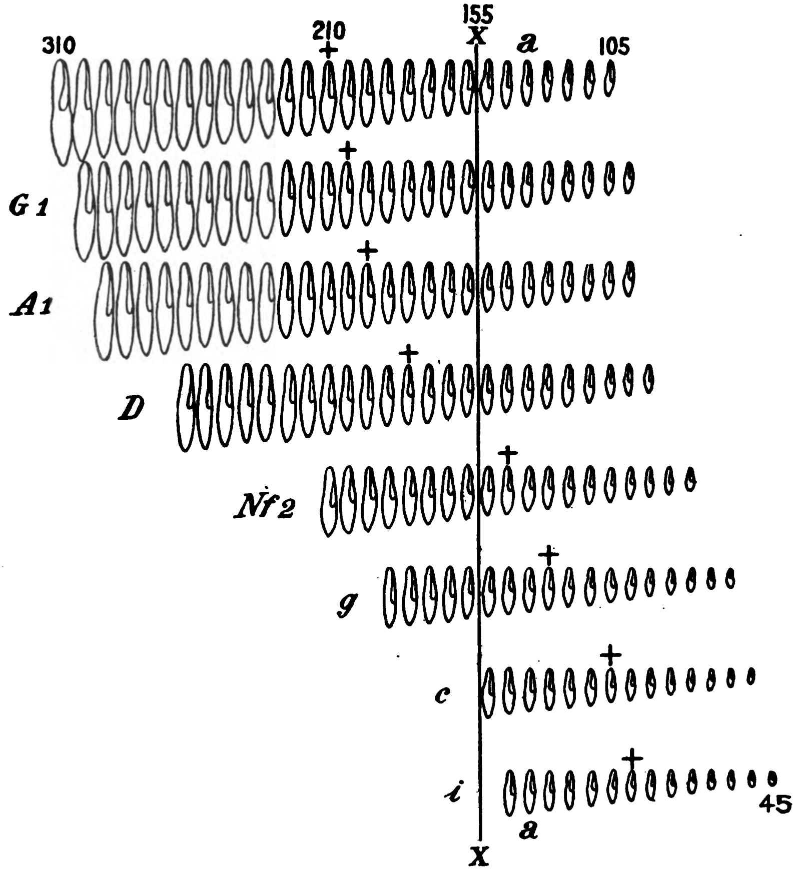

FIG. 1.—Graphic illustration of the range of fluctuations of each of the eight pure races of Paramecium studied by Jennings. (Reproduced from the American Naturalist.)

Selection here consists simply in isolating already existing races. It produces nothing new. * * *

Systematic and continued selection is without effect in a pure race, and in a mixture of races its effect consists in isolating the existing races, not in producing anything new.

Similar work with identically the same result has been done on hydra by Elise Hanel[a] and by M. A. Barber[a] on yeasts and bacteria. In Barber's work there were some exceptional cases which will be mentioned later. He found many races of each, but each race was constant, with the exceptions noted below. Long-continued selection had no effect in changing one of these races. Barber also studied individuals having various peculiarities. While the vast majority of these peculiarities behaved exactly as Jennings found them to do in Paramecium, he did find a few cases within a pure race (that is, in the descendants of a single individual) that transmitted their peculiarities to their descendants. Here we have actual evolutionary change in a race. Races of yeast were produced having cells of different form from the parent type and races of bacteria composed of longer rods than the parents, but such cases were extremely rare. Thus we must assume that there are occasionally permanent evolutionary changes. As to the amount of change in such cases we can get some information from Jennings's races of Paramecium, assuming, of course, that the differences between the various races have come about by evolutionary change. The difference between the average size of the two smallest races of Paramecium studied by Jennings was only 0.00028 inch, yet the progeny of any individual, large or small, in either of these two races, accurately maintained this difference between the races. The important point in all this is that when we are dealing with individuals of a pure race, or, as Webber calls them, a "clonal" race of variety—that is, individuals descended from a single individual by vegetative propagation—except for those very rare cases in which positive evolutionary change occurs the fluctuating differences between individuals have absolutely no bearing on the evolutionary process. According to Jennings there seems little doubt that this is true for organisms in general. He says:

> In Paramecium, in the extensive study of many races for hundreds of generations by exact statistical and experimental methods, not one single instance was observed of variation in the sense of an actual change in the race.
>
> So far as the evidence goes every race is essentially the same throughout the work and may have been the same for unnumbered ages.

Jennings emphasizes the fact that real evolutionary changes do not occur often or easily. "The fundamental constitution of the race is resistant to all sorts of influences. It changes only in excessively rare instances and for unknown causes."

In summarizing his conclusions, Jennings makes the following statement: "Until some one can show that selection is effective within pure lines it is only a statement of fact to say that all the experimental evidence we have is against this."

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[a] Cited by Jennings in American Naturalist, June, 1909.

The following statement is made by Dr. Raymond Pearl and Mr. Frank M. Surface in Bulletin No. 166 of the Maine Agricultural Experiment Station:

> There is a rapidly accumulating mass of evidence that the chief, if not the entire, function of selection in breeding is to isolate pure strains from a mixed population. It is found in actual experience impossible to bring about by selection improvement beyond the point already existing in the pure (isolated) strain at the beginning.

These writers do not here distinguish between the effect of selection in self-fertilized and cross-fertilized species, but what is said does apply to close-fertilized species strictly, where hybridizing is not practiced, and with certain limitations it also applies to cross-fertilized species, as will be seen later.

If the conclusion that selection of fluctuating variations is without effect is correct, then it follows that after we have by trial found the best individuals in a crop propagated vegetatively we have gone as far as selection enables us to go, except as immediately stated below.

But there is a second type of variation in vegetatively propagated crops which can be affected by selection. Each individual plant is endowed with a certain number of hereditary characters. These characters may or may not come to complete development under given environmental conditions, or some of them may reach complete development while others may fail to do so. In so far as this failure to develop is due solely to environmental conditions selection is without power to modify the crop. But it would appear that from time to time, or perhaps more or less continuously, changes are going on with reference to these hereditary characters by which their tendency to develop under given conditions changes; so that in a crop like potatoes we may in time get a good many varieties from the descendants of a single individual. But these varieties, in the main, arise by certain hereditary characters becoming latent or possibly in some cases disappearing altogether. Again, it may be that the tuber with which we start a race may have a good many latent characters in it whose tendency to develop may subsequently increase, so that occasionally we get a variety which differs from that with which we started by the development of certain characters which were not patent in our original stock. For instance, a white variety may produce tubers with colored skin. Color is especially likely in white varieties to occur in the vicinity of the eyes of the tuber.

The more usual variation which occurs in such cases is for characters that are present to become latent, so that we are more likely to get light color or white from colored stock.

What has been said about variation in vegetatively propagated plants applies also to bud variations, or the so-called "bud sports."

In nearly all cases these sports differ from the plant on which they originated by lack of characters that are visible in the mother plant. Occasionally, however, the reverse is true. But when a new character appears in a bud sport it is in nearly all cases a character common to the species, which was presumably latent in the mother plant.

The Ethel Maule dahlia furnishes what appears to be an example. This is sold as pure white. Mr. W. A. Andrews, of Washington, D. C., has grown this dahlia for four years. Last year (1908) one of the plants produced flowers having a decided pink tinge, especially in the center of the flowers. This year he has several of the plants produced (by division) from the pink-flowered one of last year, and all of them show the pink color. All the plants of this variety in Mr. Andrews's garden have been propagated by division from a single plant obtained four years ago. Presumably the pink color is latent in the original stock and has been partially revived in these pink-flowered individuals.

In those vegetatively propagated plants where variation occurs by hereditary characters becoming latent—and this type of variation seems to be quite common, especially in potatoes—selection of seed is of great importance. In this case selection enables the breeder to keep his stock up to standard, at least much longer than would be the case without selection, and where variation occurs by the development of characters which were previously latent it enables him to preserve such variations when they are of value.

The results of the application of the principles here stated to the selection of seed potatoes have been in some cases quite marked. For instance, a potato grower in Michigan some years ago began the practice of digging by hand enough potatoes for seed and saving only those hills that had six or more merchantable tubers and no small tubers. When he first began this practice he found only sixteen hills out of each hundred dug that came up to his standard, but after he had continued the practice for five years the number of such hills had risen to seventy in a hundred. Under the direction of Mr. L. G. Dodge, of the Office of Farm Management, several New England potato growers have been applying these principles for two years past. The first year there was an average of about eight hills per hundred that came up to standard. The second year from seventeen to twenty hills met the conditions. This is as far as the experiment has proceeded at the present time. Some work done on potatoes by Mr. C. W. Waid, of the Ohio Agricultural Experiment Station, has given similar results. In this work, starting with the same original lot of tubers, three strains were grown, as follows: (1) Seed from high-yielding hills, (2) seed from low-yielding hills, and (3) unselected seed. Taking the yield of the unselected seed as a basis, the results were as follows:

Source of seed.	1904.	1905.	1906.	1907.[a]	1908.[b]
From high-yielding hills	122	127	147	125	171
From unselected hills	100	100	100	100	100
From low-yielding hills	70	55	77	66	91

[a] See Report, American Breeders' Association, vol. 3, p. 191 et seq.
[b] See Circular No. 90, Ohio Agricultural Experiment Station.

SELF-FERTILIZED SPECIES.

The effect of selection on self-fertilized species, such as wheat, barley, and oats, is essentially the same as it is on species propagated vegetatively. Doctor Nilsson in his remarkable work at Svalöf, Sweden, has many times taken an unselected lot of seed from some cultivated variety of wheat or oats and planted each seed individually to study the character of the plants produced. He rarely finds two plants exactly alike. But when he saves the seeds from these plants separately the next year the progeny of each plant is, as a rule, found to be so much like the parent plant as to be indistinguishable from it except for such fluctuations as may be due to environmental influences only.

Occasionally in work of this kind a plant is found which is not homozygote in all its characters. In other words, it is not absolutely pure bred. These plants split up in the next generation according to the law of recombination. Furthermore, their presence indicates that there is occasionally cross-fertilization in wheat and oats, so that ultimately in a wheat field there may be found practically every possible combination of all the characters present in the field, and in time every one of these combinations will come to exist in some individuals in homozygote form; for, as will be seen later, a self-fertilized plant tends to split up into all the fixed forms which can be made from the various combinations of the characters present in it.

Neglecting for the present the occasional cross-fertilizations in a field of wheat or oats and the resulting heterozygote plants that are produced in this manner, which will be considered under the next heading, selection without cross-fertilization in self-fertilized species can have no effect except to enable the breeder to find those individuals which are best among the population with which he is dealing. After he has found these individuals he can not improve them by selection. On the other hand, he may be able to hold them up to a high standard by means of selection, for presumably, as in the case of potatoes, the hereditary characters present in wheat may change in their tendency to develop. Especially may characters that are present get into the habit of failing to develop and thus give rise to inferior plants in the progeny of what was originally a high-class individual.

While experimental evidence for the above statements is not as plentiful as it ought to be, Doctor Nilsson has done so much work along this line that the propositions enunciated may be considered practically established. Professor Johannsen, of Copenhagen, has done a great deal of work of the same kind with exactly the same results. At the 1906 Genetic Conference in London he said, "In a population containing only one single type the selection of fluctuations has no action at all." Johannsen has several races of beans which he has grown pure for several years and which are fully homozygote. He has fully tested the effect of selection on certain seed characters of these beans. Speaking of the results,[a] he says, "Selection for weight, for absolute length, or relative breadth has had absolutely no observable influence on these characters." Johannsen has obtained similar results with barley.

After what we have seen to be true in vegetatively propagated races it should not be surprising that similar results occur in self-fertilized races, for although such races go through the form of recombining the characters when they produce seed, the two members of each pair of characters being exactly alike, we get no new combinations, so that reproduction by seed in completely homozygous strains differs little, if at all, in its results from vegetative propagation.

The fact that in a field of a self-fertilized crop a very large majority of the plants are perfectly fixed in their hereditary characters and will reproduce themselves with almost absolute fidelity from seed has led a good many biologists to consider every one of these plants which differs from its neighbors in any way to be what they call "elementary species." They overlook the fact that these forms are fixed simply because they are homozygote in all their characters and would behave in exactly the same manner whether the evolutionary changes that produced them are either very slow and gradual or occur suddenly at long intervals.

The problem, then, in selecting self-fertilized plants is to find the best individuals and propagate from them. There are two ways of selecting such plants, which give somewhat different results. One of these we may term "mass selection," the other "individual selection."

MASS SELECTION.

Mass selection is that form of selection in which a number of superior plants or parts of plants are chosen but their seed is not kept separate. It may happen that some of the selections thus made are superior because they have been grown under very favorable environment and that another year when the environment is less favorable they may prove to be very inferior. Others may prove to be superior under a wider range of environmental conditions, so that from year to year they will be superior. The next year mass selection would be mostly from those plants which are what we may call permanently superior, together with a few of those which merely happen to be superior under the given conditions. The continuation of mass selection thus tends to improve from year to year the general character of the crop, but it does this by the gradual elimination of the progeny of those plants which are not superior except under very favorable conditions. This gradual improvement that occurs in mass selection has misled biologists and plant breeders generally into believing that selection could affect fluctuating variation.

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[a] Zeitschrift für Induktive Abstammungs- und Vererbungslehre. September, 1908, p. 2.

The effect of mass selection of self-fertilized crops is well illustrated by some of Prof. C. A. Zavitz's work at Guelph, Ontario, Canada. In his annual report for 1905 he gives the results of sixteen years' continuous mass selection on oats and barley. These are given below. For convenience, his results obtained by similar methods with potatoes are also given here. It will be noticed that mass selection has the same effect in self-fertilized wheat and oats as in potatoes, which are propagated vegetatively.

TABLE III.—*Average yields by four-year periods, in bushels per acre, of oats, barley, and potatoes, showing the effect of mass selection on self-fertilized and on vegetatively propagated crops.*

Crops.	1890–1893.	1894–1897.	1898–1901.	1902–1905.
	Bushels.	*Bushels.*	*Bushels.*	*Bushels.*
Oats, average for 8 varieties	74	79	83	100
Barley, average for 8 varieties	50	54	63	63
Potatoes, average for 7 varieties	120	216	218	249

The very marked effect in the case of potatoes is probably due to degeneration which had occurred in many vegetative strains before the selection began, the progeny of these degenerate strains being gradually eliminated by mass selection.

The Mandscheuri barley, now so largely grown in Ontario, is descended from a single pound of seed obtained from Prussia in 1889. Of this variety 567,000 acres were grown in Ontario in 1908. Since the introduction of Mandscheuri, the barley crop of Ontario has increased in value from $4,800,000 to $12,900,000, and this is in part due to the larger yielding power of this variety. The greater profit due to larger yields has caused an increase in acreage.

INDIVIDUAL SELECTION.

In the form known as individual selection we start with superior plants and keep their seeds separate. This enables us very quickly to determine which of the original selections are superior under a wide range of conditions, so that within a few years we can determine which of our original selections represent the best strains in the variety. Then by propagating from them and by continuously selecting to avoid saving any plants which may be deteriorating from hereditary characters becoming latent, we can maintain the variety at a high standard. But it must be remembered that we can not increase the superiority of a pure strain by selection except in those comparatively rare cases where characters that were latent in our original selection change in their tendency to develop and happen to increase the superiority of the strain.

That latent characters may reappear in a variety is shown by the following facts. Sometimes, in varieties of potatoes having white skin, tubers are found which have purplish or red skin, at least over part of the surface, and especially about the eyes. Bud sports sometimes exhibit characters not apparent in the parent stock, but common to other varieties of the species. In Doctor Nilsson's work at Svalöf, Sweden, black or yellow oats occur at wide intervals in white varieties. All these facts indicate that latent characters occasionally become patent.

We have already referred to the effect of mass selection on barley at the Ontario Agricultural Experiment Station. Professor Zavitz has also used individual selection on varieties of this crop. In 1903 he selected 9,972 grains of the Mandscheuri barley and planted them individually. Seed of 33 of these were planted separately in 1904. By 1908 all but three of these strains had been discarded. One of these, known as "O.A.C. No. 21," which outyields the original variety, is now rapidly replacing the latter on Ontario farms.

The selection at the Minnesota station, begun by Prof. Willet M. Hays, is individual selection. The seed of each plant, to serve as the original parent of a strain, is saved separately, so that the yielding power of pure strains is determined by several years' test of successive generations of their self-pollinating progeny. The best of these are finally brought into culture. This method enables the breeder to secure the best strains present in the seed with which he starts, or, as Professor Hays puts it, it enables the breeder to find those plants having the highest "centgener" power; that is, the power of producing strains with maximum yields under the widest range of environmental conditions. Some of the wheats obtained in this manner at the Minnesota station have proved decidedly superior to the original mixed stock from which they were isolated.

In these homozygote forms, which constitute the major part of a field of any crop which habitually self-fertilizes, there is little, if any, more variation than in plants which are propagated vegetatively.

CROSS-FERTILIZED SPECIES.

The effect of individual selection on cross-fertilized species, such as corn, is very different from what it is in self-fertilized species. Here the plants chosen are more or less cross-fertilized with other plants and the seeds obtained from a single plant are not all alike in content of hereditary characters. Hence we may get distinct differences in the individuals grown from this seed. Either mass selection or individual selection in a crop of this character may make decided changes in it for the reason that, in the seed of every plant, combinations of hereditary characters will occur that are unlike those in the original plants selected. Some of these may be superior to the original plants. For instance, the plant with which we start may be heterozygote with reference to a particular character which we will call "*A*." That is, it inherited from one of its parents the presence of this character and from the other its absence. Its formula with reference to this character would therefore be *Aa*. Such a plant will produce progeny one-fourth of which has the formula *AA*, one-half *Aa*, and one-fourth *aa*. Now, the combination *AA* may be superior to *Aa* and *aa*, so that in the seed of our selection we may get something better than the plant selected. On the other hand, we may also get something not so good. Selection alone, therefore, enables us to make positive improvements in crops which regularly cross-fertilize.

The work done on the corn plant at the Illinois Agricultural Experiment Station is perhaps the best illustration of the effect of selection on crops that cross-fertilize. Bulletin 128 of that station gives the results of ten years' selection of corn for high and low oil content and for high and low protein content. Some of these results are given in Table IV.

TABLE IV.—*Effect of selection in a cross-fertilized species. The figures of column 2 give differences in percentage content of oil between two strains of corn of similar origin, one selected for high and one for low oil content. Column 3 gives similar differences between two other strains selected, one for high and the other for low protein content.*

Years.	Oil differences.	Protein differences.
	Per cent.	*Per cent.*
1896	0.00	0.00
1897	.67	.55
1898	1.16	.50
1899	1.82	1.60
1900	2.55	2.98
1901	2.66	4.08
1902	3.39	4.12
1903	3.53	4.52
1904	4.08	5.76
1905	4.71	6.15
1906	4.71	5.62

Bulletin 132 of the same station gives the results of six years' selection of corn for high and low ears. See Table V.

TABLE V.—*Difference between two strains of corn selected for ears high or low on stalk.*

Years.	Difference in height of ears.	Difference in number of internodes in stalks.
	Inches.	*Number.*
1903	13.6	1.5
1904	12.0	1.5
1905	21.7	1.8
1906	31.1	4.1
1907	39.2	3.3
1908	34.2	4.0

Another instance of the effect produced on a species which is partially cross-fertilized is seen in some interesting work of Professor von Rümker at the Breslau Experiment Station in Germany. This work was done on rye, in which species more or less cross-fertilization occurs. By continued individual selection for color of seed Professor von Rümker finally obtained several strains of markedly different color. Yellow color was more difficult to fix than green. This is probably due to the compound nature of the yellow color from the Mendelian standpoint. Some interesting cases of correlation were found in this work. Green-colored seeds produced stronger stalks; brown seeds were less winter hardy. It was found that the selection must be continued in order to maintain the characters for which the selections were made. It is doubtful if these results could have been obtained in a strictly self-fertilized species.

The reason why selection produces these effects on cross-fertilized plants is seen in the following: Suppose we start with a corn plant that is heterozygote for yellow and white corn and for starchy and sweet corn characters. The presence of yellow may be represented by Y, the absence of yellow (that is, white) by y; the presence of starch-forming character by S, and its absence (that is, sweet-corn character) by s. Figure 2 shows the nine different types of corn which would be produced by the individuals. If, now, we plant all the seed produced by these nine types of corn and plant them where they can freely cross-fertilize, but where they will not cross with other kinds of corn, the next year we shall again get these same nine types in approximately the same proportion, and so on indefinitely. This is shown graphically in figure 2, which shows what happens when we have a mixture of types that cross-fertilize with each other. This figure will be understood when it is explained that the space between any two adjacent horizontal lines represents the proportion of the population of the type represented by the formula in that space. Here each of the nine spaces maintains the same width from generation to generation. This means that each of the nine types present tends to remain in the same proportion from generation to generation under these oonditions.

Referring again to figure 2, and supposing that we desire to select from this mixed population and perpetuate the type *YYSS*—that is, pure yellow starch-forming corn—we would at once discard the following forms: *YYss*, *Yyss*, *yySS*, *yySs*, and *yyss*. All of these would either be white or of the sweet type, or both. Discarding all these types that are not yellow starch-forming types, we would still have left the second, fourth, and fifth types shown in figure 2, all of which would be yellow and would have starchy grains, because the presence of these two characters is dominant over their absence, and these types heterozygote for one or both of these characters can not be distinguished by inspection from type 1, which is the type we wish to perpetuate.

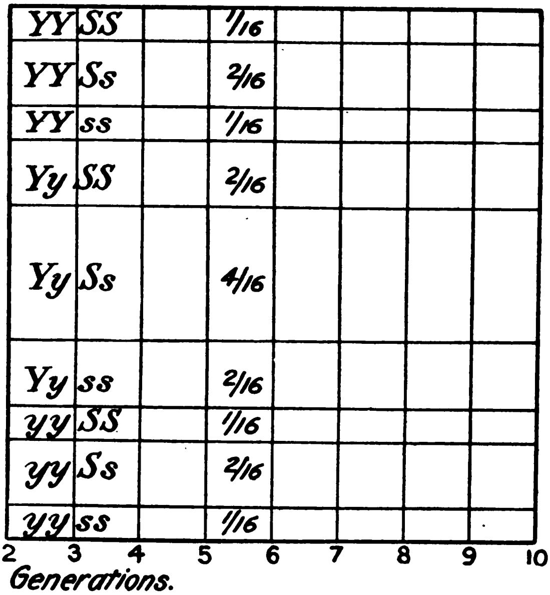

FIG. 2.—Graphic illustration of ten generations of corn with no selection, the first generation of which is *YySs*. The proportion of each type is indicated by the vertical space between the horizontal lines above and below the type symbols. Thus, *YYSS* is one-sixteenth of the whole population. Under the conditions mentioned each type tends to remain in the same proportion from year to year.

Selecting for seed those plants which do have yellow, starchy grains—that is, types 1, 2, 4, and 5 of figure 2—and planting them where they can cross with each other but not with other corn, the next year the proportion of each of the nine types that would appear would be as shown in Table VI, column 3. If we make the same kind of selection again the next year the proportions of the nine types would be as in column 4. Table VI shows the results that would be obtained at the end of the sixth generation by this kind of selection in a cross-fertilized crop.

TABLE VI.—*Types and their percentages in the descendants of YySs for several generations with cross-fertilization and continued selection to type YYSS. Regarding YySs as the first generation, we have:*

Types.	Generations.				
	2.	3.	4.	5.	6.
	P. ct.	*P. ct.*	*P. ct.*	*P. ct.*	*P. ct.*
YYSS	6.25	19.8	31.6	41.0	48.2
YYSs	12.50	19.8	21.1	20.5	19.3
YYss	6.25	4.9	3.5	2.6	1.9
YySS	12.50	19.8	21.1	20.5	19.3
YySs	25.00	19.8	14.0	10.2	7.7
Yyss	12.50	4.9	2.3	1.3	0.8
yySS	6.25	4.9	3.5	2.6	1.9
yySs	12.50	4.9	2.3	1.3	0.8
yyss	6.25	1.2	0.4	0.2	0.1

The type *YYSS* gradually increases until in the sixth generation it constitutes 48 per cent of the crop. This type, together with types *YYSs*, *YySS*, and *YySs*, all of which appear to be the same as *YYSS*, constitutes 94.5 per cent of the sixth generation. Thus in cross-fertilized crops mass selection to a given type gradually establishes that type, not so rapidly, however, as it does in self-fertilized species, after hybridization.

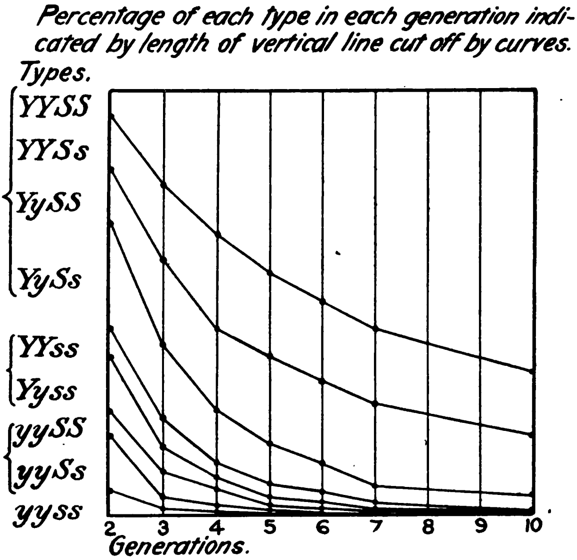

FIG. 3.—Graphic illustration of the effect of mass selection in cross-fertilized species. Selection for type *YYSS*; types so arranged as to bring together those that resemble each other. The proportion of type *YYSS* from generation to generation is shown by the space between the top horizontal line and the upper curved line. It would seem to increase from generation to generation. The proportion of type *YYSs* from generation to generation is indicated by the vertical width of the space between the two upper curved lines. Similarly, the space beginning opposite each type formula indicates the proportion of that type present from generation to generation.

Figure 3 shows the same thing graphically for ten generations. In this figure the space between the top curved line and the horizontal line at the top of the diagram shows the proportion of the type *YYSS* present from generation to generation. It is seen that in the second generation only a small proportion (one-sixteenth) of type *YYSS* is present. In generation six, almost exactly half the population is *YYSS*, while in generation ten this type constitutes about 65 per cent of the whole. The proportion of type *YYSs* present from generation to generation is indicated by the space between the two upper curved lines. It is seen that this type increases slightly until the fourth generation, after which it gradually decreases. The five types at the bottom of the figure decrease very rapidly from the second generation on, so that by the tenth generation they have almost disappeared, and the population is made up almost entirely of yellow, starch-producing types which are either pure (type *YYSS*) or heterozygote (types *YYSs*, *YySS*, and *YySs*) for one or both of the characters with which we are dealing. Table VI and figure 3 thus illustrate the effect of mass selection on crops which cross-fertilize, and this effect is seen to be a gradual approach toward the type selected.

Evidently the limit of the effect of selection in a case of this kind is reached when practically the whole crop is homozygote for the character selected. No further advance can be made by selection, and it must be remembered that in order to hold the crop at this high degree of excellence selection must be continued, because here and there plants will vary by certain characters becoming latent and thus reducing the general average of superiority in the strain.

The problem of improving cross-fertilized species or varieties by selection to a particular type is complicated by the fact that in plants which ordinarily cross-fertilize we are apt to lose vigor when we get our plants too much alike. That is, these plants have been used to cross-breeding, and when we get our population very uniform, which is only another way of saying get them very close kin to each other, the yield is liable to run down because of this very uniformity. There is some question, therefore, whether in a cross-fertilized crop we should attempt to get great uniformity.

We can partially overcome this difficulty by each year selecting the best individuals we can find and planting them in alternate rows so as to get as much cross-fertilization as possible. In corn the ear-row method of breeding permits this to be done. The methods adopted by some of the best corn breeders in the country at the present time are essentially as follows: Every year they go through the seed plot and also through the cornfield and select the best ears they can find to use in the seed plot the next year. As many ears are selected as there will be rows in the seed plot. In this way there will be the normal cross-fertilization in the seed plot with the resulting vigor that comes from cross-fertilization. Careful account is kept of the yield of each of the rows in the seed plot, so that the breeder may learn what ears selected the year before tend to produce the best yields. This enables him the next year when he goes to the seed plot or the cornfield to select seed to know what types to look for, and it is probably wise, from the standpoint of yield, to select each year two or three types, if not more, provided they all yield well, so as to insure as much cross-fertilization as possible in the seed plot.

The fact is, we know very little indeed about the relation between yield of corn and type of ear. Prof. A. E. Grantham, of the Delaware Agricultural Experiment Station, recently called the writer's attention to the fact that in communities that have been unaffected by modern ideas about corn breeding, the best ears of corn are usually of the so-called "slick" type. He suggests that this may be a case of the survival of the fittest. Farmers have from year to year selected sound ears for seed, paying little or no attention to type. The prevalence of slick ears may therefore represent a case of the survival of the fittest. In testing local varieties of corn unaffected by modern ideas of selection alongside of the improved varieties, Professor Grantham states that the local varieties yield about as well as the others. The writer can partially verify this statement for southwestern Missouri. On his own farm there is a variety of corn that has been grown there for at least thirty years. The best ears of this variety are decidedly slick; on good land it has yielded 80 bushels per acre. A single year's test of one of the noted improved varieties in comparison with this local one indicates that the improved variety will outyield the other considerably, but it is important to note that the improved variety, although selected for excellence for fifty years, has never been selected for uniformity of type and has not a few slick ears in it.

The amount of careful investigation that this question of relation of type to yield has received is wholly inadequate. It ought to receive careful attention at the hands of our best investigators.

There is another method of breeding open-pollinated crops, like corn, that, while it has not been extensively tried, seems to deserve consideration. This method consists of maintaining two pure strains which are not close kin, and raising each year seed which is a cross between these two varieties and using this seed for the field crop the next year. This method was first proposed by Dr. G. H. Shull[a] in an article read before the American Breeders' Association at its Washington meeting in January, 1908. Shull's results have been confirmed by Dr. E. M. East, of the Connecticut Agricultural Experiment Station, whose work is referred to later in these pages. A similar plan was recently proposed by Mr. G. N. Collins, of this Bureau, in a bulletin entitled "The Importance of Broad Breeding in Corn."[b]

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[a] See Report, American Breeders' Association, vol. 4.

[b] Since the above was written, Mr. Charles P. Hartley, of this Bureau, has called the attention of the writer to some recommendations made in 1893 and 1894 by Prof. G. E. Morrow and his assistant, Mr. F. B. Gardner, of the Illinois Agricultural Experiment Station. In Bulletin 25 of the Illinois station these investigators say: "The fact that increased yields can be obtained by crossing two varieties is pretty certainly

A representative of the Office of Farm Management several years ago reported that in a certain community in one of the Western States farmers generally planted white and yellow corn in alternate rows in their seed patches. In this way they were sure of getting the vigor that comes from hybridization in the corn to be used for the general field crop the next year. Some of the farmers simply planted their whole field in alternate rows of yellow and white corn, and the next year used seed selected out of this field for planting. The next year they would go back again and get pure yellow and pure white corn from some outside source and start over again, but this is a crude method which gets advantage of the hybridization only every other year. A better plan would be to get two good varieties of corn, both known to be adapted to the conditions, and plant a seed patch somewhat more than twice as large as needed to produce seed for the fields the next year, planting the two varieties in alternate rows in the seed patch. In one-half of the seed patch one of these varieties is detasseled and in the other half the other variety is detasseled. On both sides of the seed plot the detasseled stalks would bear only hybrid grains. On the other hand, the stalks that were not detasseled would be fertilized by pollen from stalks of the same variety, except in the middle of the patch, where there would be some cross-pollination between the two varieties. At harvest time pure seed of the two varieties is selected for the next year's seed plot from the extreme sides of the plot, where there has presumably been no cross-fertilization between the two varieties, while seed for the general field crop is selected from the detasseled stalks

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established, and a few farmers are changing their practice accordingly. This is quite easily done, by planting in one row one variety, and in the next another variety, and removing the tassels of the one as soon as they appear. The ears forming on the rows having the tassels removed will be fertilized with pollen from the other rows, thus producing a direct cross between the two varieties. The seed should be selected from the rows having the tassels removed, and the experiments indicate that it will pretty certainly give a larger yield than the average of the parent varieties when planted under like conditions."

In a comparison of five crosses with the average yields of their parents the average increase in yield due to having crossbred seed in the experiments above referred to was 9.5 bushels.

Again, in Bulletin 31 of the Illinois Agricultural Experiment Station the same authors make this recommendation: "Farmers can produce crossbred seed in considerable quantities in the following manner: Plant with one variety in one planter box and another variety in the other. Remove the tassels of one variety before they begin to shed pollen, and the shoots of the same will be fertilized with pollen from the other variety, thus producing a direct cross. The seed should be selected from the rows from which the tassels have been removed."

In three out of four comparisons between crosses and their parents reported in the bulletin last referred to the crosses outyielded the parents, the average increase being 2.3 bushels per acre in favor of the crosses.

from the whole plot. This method would take advantage of the well-known vigor which arises when two varieties of corn are crossed.

Shull has recently proposed a plan somewhat similar to the above, and one which is really an improvement on it in one respect, but not so good in another.[a] He suggests using two pure strains, planting one of them off by itself to get pure seed of it for the seed patches the next year, while at the same time another seed patch for growing field seed is planted of alternate rows of the two varieties. In this patch all the stalks of the variety grown alone in the other patch are to be detasseled. All the seed produced by the detasseled stalks will be heterozygote, while all the seed on the remaining stalks will be pure bred of the other strain from that planted alone in the smaller patch. The principal difficulty with this plan is that of finding isolated spots for two seed patches instead of for one, as in the plan in which the two varieties are both planted in alternate rows in one patch. In Shull's plan the two strains could be kept practically pure; in the other plan they would mix to a slight extent.

HYBRIDIZATION AND SELECTION.

We have been considering only the effect of selection without deliberate hybridization or cross-fertilization, except such as occurs naturally in certain of the crops considered. We shall now consider the application of artificial cross-fertilization and subsequent selection to the art of improving farm crops.

As in the case of selection alone, the methods and results differ for vegetatively propagated, close-fertilized, and cross-fertilized crops.

VEGETATIVELY PROPAGATED CROPS.

It is perhaps easier to secure the advantage of hybridization in vegetatively propagated crops, such as fruits, berries, potatoes, hops, and sugar cane, than it is from those crops that reproduce from seed. The reason for this is that some of the heterozygote forms which occur in the first generation of the hybrid may be highly valuable, and these heterozygote forms can be propagated true to type because they are not propagated from seed. For instance, suppose we cross two varieties of apples or potatoes and get in the first generation a plant from which can be made a valuable new variety. All that is necessary is to propagate this new variety by cuttings.

In the case of potatoes very little hybridizing has been done. The seedling plants do not attain their full development until propagated from the tubers for two or three years. It is therefore necessary gradually to eliminate the poorer stocks and to grow for some time a good many of the forms which result from crossing, to see whether or not they are valuable.

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[a] See Report, American Breeders' Association, vol. 5.

It must also be remembered that nearly all crops which are propagated vegetatively belong to the class of crops which naturally cross-fertilize; so that when we make a cross between two of them we are really crossing things that are themselves many times hybrid. For instance, a Baldwin apple tree is heterozygote for a good many of its characters. For this reason it produces many kinds of pollen and ovules, and when we use the Baldwin in a cross we get numerous different varieties in the first generation, while if the two varieties used in the cross were completely homozygote for all their characters all the first-generation hybrids would be alike.

SELF-FERTILIZED SPECIES.

The principles involved in the hybridization and subsequent selection to type of close-fertilized species, like wheat and oats, have already been stated in more or less detail, but some additional points need to be brought out. In utilizing hybridization in close-fertilized crops the first problem is to select suitable forms for hybridization. Sometimes these forms are already at hand and well known. The real object to be accomplished by hybridization in this case is to make use of the law of recombination, by which we can bring together in one variety certain valuable characteristics which are found scattered among two or more varieties which we may have at hand or can secure. Take, for instance, the problem which presented itself, while the writer was agriculturist at the Washington Agricultural Experiment Station, in connection with wheat growing in eastern Washington. When the writer first went to Pullman, where the experiment station is located, the farmers had been growing wheat in that section for twenty-five or thirty years. They had tested many hundreds of varieties, but found very few of them adapted to local conditions. Only three varieties had at that time come into general use, and these three were each more or less restricted to definite areas of different rainfall. For instance, where the rainfall was 10 or 12 inches almost the only variety grown at that time was Bluestem (not the hairy chaffed Bluestem of the middle Northwestern States). This was grown for two reasons. In the first place, it was one of the very few varieties found that would grow tall enough to cut with so little rainfall. In the second place, it produced a very superior quality of flour, and millers paid about 3 cents a bushel more for it than for other varieties. But this tall-growing variety could not be grown where the rainfall was 20 inches or more, because it would fall down if the season was at all unfavorable. Where the rainfall was about 18 inches a variety of club wheat known as "Red Chaff" was very widely grown, while in those sections where the rainfall was 22 inches or more the prevailing variety was another club wheat known as "Little Club."

The growers of Red Chaff gave as their reasons for using this variety that it stood up better than Bluestem and yielded more than Little Club, while the growers of Little Club stated that this was the only variety they had ever found that would stand up and hold its grain under their conditions.

It happens that all three of these varieties are spring wheats, but long experience has shown that sowing them in the fall would, in favorable seasons, produce yields 30 to 60 per cent greater than spring sowing. Hence, all three varieties were generally sown in the fall, but they would frequently freeze out to a greater or lesser extent. There was therefore an insistent demand for winter wheat. The writer had collected from various parts of the world an extensive series of winter wheat varieties, and in 1899 a large number of these varieties had been grown for five years. Many of them were perfectly hardy and made enormous yields in favorable seasons, but they were inclined to straw-fall and to shatter their grain as soon as they were ripe; so that it did not seem advisable to recommend any of them to the farmers.

At that time Mendelian principles were unknown in this country and had been forgotten in Europe, so that the writer had intuition alone to guide him in his attempts to produce a variety of wheat adapted to local conditions. By chance these intuitions proved to be correct and led to the discovery of the law of recombination previously stated. Fortunately, the work proceeded from the beginning just as it would have done had the writer had full knowledge of the law of recombination, for the law was discovered in time to use it as soon as it could have been used in this work.

Eleven of the best yielding winter varieties were crossed with the Little Club and the Red Chaff varieties (the Bluestem could not be successfully grown at Pullman, where the rainfall was about 22 inches). Among the first-generation hybrids there were, therefore, eleven kinds. The seed of each hybrid plant was saved separately, so that the next year we had as many plots as we had hybrid plants the year before.

The object of this hybridization work was to combine the winter hardiness of one class of varieties with the stiff straw and the tightly closed chaff of the other varieties. We now understand why this combination succeeded in every one of the crosses, so that from each of them resulted new and fixed varieties of wheat combining the characteristics mentioned. As was to be expected, some of the new varieties proved to be much more productive than others.

The writer severed his connection with the Washington Agricultural Experiment Station at the beginning of 1902, but his successor and his assistants continued the work with the hybrid wheats, and this work is still in progress, being conducted by Mr. C. W. Lawrence, of the Washington station.

Three of these hybrid varieties (which had been fixed by proper selection, methods of which are outlined below) were distributed in small quantities to the farmers in the fall of 1907, after having been carefully tested at the experiment station as to their yielding power. In the fall of 1908, 39,000 acres of these new varieties were reported as being sown by the farmers in eastern Washington. In two more years there will doubtless be seed enough for all.

The case just cited illustrates one in which hybridization furnishes a means of securing new and valuable varieties, namely, the case where certain valuable characteristics are found in different varieties and it is desirable to unite these characteristics. Such cases would exist at most plant-breeding stations. Doctor Nilsson, at Svalöf, has made extended use of these principles in producing new varieties of cereals at his station. The first task is to select the varieties having desirable characteristics. Frequently some of the characteristics will be found in varieties that are otherwise worthless, so far as their use as field crops is concerned, so that in breeding work a variety should not be rejected because of a single weakness. It is legitimate to use an inferior variety in crossing, provided it has some valuable characteristics.

In working with self-fertilized crops the principles involved for the first two years are exactly the same as those in cross-fertilized crops illustrated in Table VI. The first generation of the hybrid is heterozygote for all those characteristics in which the two parent varieties differ. Where the parents differ in a great many respects the problem becomes quite complex, for the number of types that will be produced in the second generation is equal to 2^n, n being the number of points in which the two parents differ. Thus, when they differ in one particular, that is, when we have one pair of allelomorphs to deal with, there are two distinct types in the second generation of the hybrid. If the parents differ in two respects, we have $2^2=4$ distinct types in F_2 (the second generation of the hybrid). Three differences give $2^3=8$ types, and so on. The figures given above assume that in each pair of allelomorphs there is complete dominance, so that the heterozygotes can not be distinguished from the pure dominants. If the heterozygotes can be distinguished, then the number of visibly different types in the second generation is 3^n. In fact, in so far as their content of hereditary characters is concerned there are always 3^n types in the second generation when the varieties crossed differ in *n* particulars. In many cases we can neglect a great many of these differences, because they are immaterial and deal only with those character pairs which are important. Table VI shows what occurs when the parents differ in two respects. The first generation is heterozygote with respect to both character pairs. In the second generation nine types occur in the proportion shown in Table VI.

In the third generation we get a different result with self-fertilized plants from that obtained in cross-fertilized plants, because in self-fertilized species a heterozygote when it makes seed breaks up into one-fourth pure dominants, one-half heterozygotes, and one-fourth pure recessives; while with open-pollinated species the proportion of heterozygotes produced by heterozygotes will be larger than one-half, because of the introduction of foreign pollen.

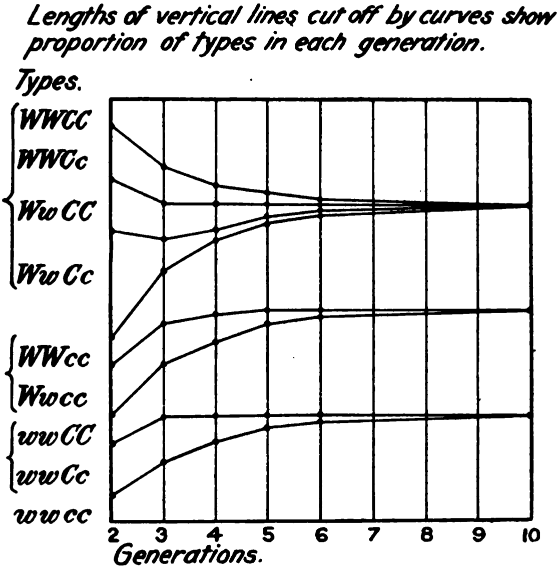

FIG. 4.—Graphic illustration of ten generations of a hybrid in a self-fertilized species without selection to type: *W*, winter character; *w*, absence of *W* (i. e., spring character); *C*, club character (short, thick heads); *c*, absence of *C* (i. e., long-head character). Types arranged so as to bring together those that resemble each other. The space between the top horizontal line and the uppermost curved line shows the proportion of type *WWCC* present from generation to generation, and the space beginning opposite each type formula shows the proportion of that type. The population ultimately consists almost entirely of the four homozygote types present.

Let us first consider what occurs in self-fertilized species if we make no selection at all among the progeny of the hybrid. Figure 4 shows what occurs in this case. Suppose the plant with which we are dealing is a hybrid between a long-headed winter wheat and a club or short-headed spring wheat. In the second generation we get the usual nine types, as seen at the left of figure 4, where *W* = winter character, *w* = spring character, *C* = club heads, and *c* = long heads. The nine types are arranged in figure 4 so as to bring together those which appear to the eye to be alike. Thus the types *WWCC*, *WWCc*, *WwCC*, and *WwCc* are all winter clubs, since *W* is dominant over *w* and *C* is dominant over *c*. *W Wcc* and *Wwcc* are long-headed winter wheats, *wwCC* and *wwCc* are spring clubs, while *wwcc* is a long-headed spring type.

The relative proportion of each of these nine types for a series of generations, from the second to the tenth, is shown in the diagram of figure 4. For instance, the proportion of type *WWCC* is indicated by the space between the top horizontal line of the diagram and the upper one of the curved lines. The generations are indicated by the figures at the bottom of the diagram. In generation two the space for type *WWCC* is narrow, constituting only one-sixteenth of the second generation. But this type increases from generation to generation until by the tenth generation it is practically one-fourth of the population; that is, when there is no selection to type.

Type *WWCc* is seen to decrease from generation to generation, as indicated by the space between the two upper curved lines. This space gradually becomes narrower, so that it has practically disappeared by the tenth generation. The space beginning opposite each type formula shows what happens to that type. It is seen that the four homozygote types *WWCC, WWcc, wwCC,* and *wwcc* gradually increase in proportion while all the heterozygote types decrease. By the tenth generation the whole population consists practically of the four homozygote types, each of them constituting practically one-fourth of the population. Only small amounts of any of the heterozygote types remain in the tenth generation. Of these four homozygote types, two of them will be just like the two parents, as far as the characters we are considering are concerned. The other two will represent new combinations of the characters under consideration; the new types are (1) winter character with club heads and (2) spring character with long heads. We may therefore in such cases (i. e., with self-fertilized crops) secure our hybrid and plant its seed for several years without any selection at all, then select out the type we want and it will be almost entirely pure; that is, nearly all the plants selected will reproduce true to type as far as the characters wanted are concerned. Then selecting individual plants of the type wanted we can quickly get plants that are homozygote with reference to practically all their characters by planting the seed of each plant separately and observing which of them do reproduce true to type.

These fixed forms which occur in the progeny of hybrids are sometimes mistakenly called "mutations." They are in no sense mutations of the sort comprehended by that much misused term as it is at present understood. They are simply recombinations of characters which, before the hybridization occurred, existed in different combinations.

After these fixed forms are obtained the same laws apply to their selection as have already been described under the effect of selection on close-fertilized forms. Generally speaking, we can not modify them by selection, but selection may be valuable as a means of holding them up to a high standard.

Reverting again to the hybrid produced by crossing long-headed winter wheat with a club-headed spring wheat we shall now consider the effects produced, first, by mass selection and, second, by individual selection in the progeny of such a hybrid. Figure 5 shows the result of mass selection for the winter club type. Since both the winter character and the club character are dominant in this cross, four of the nine types occurring in the second generation will appear to be winter club wheats. These are the upper four types of figure 5. The other five can be distinguished at once, because they will either show the long-head character or the spring character. To determine whether or not a wheat is winter or spring in character it should be planted in the spring. If it makes a crop the same season it is a spring wheat. If it waits until the next season before it heads out it is a winter wheat. The four types in the second generation which appear to be winter club wheats are those having the constitution *WWCC*, *WWCc*, *WwCC*, and *WwCc*, in which *W* stands for the winter character, *w* for the spring character, *C* for the club character, and *c* for the long-head character. The first of these four types is already fixed and will reproduce itself faithfully. The others are heterozygote with reference to one or both character pairs, and will consequently the next year produce some progeny which will be either spring or long-headed wheat, or both. Suppose, now, that in the second generation we discard everything except these four types. Figure 5 shows what the result will be. The diagram of figure 5 is easily interpreted if we understand that the space between the top horizontal line and the uppermost curved line represents type *WWCC*, the space between the two uppermost curves represents type *WWCc*, and so on. It is seen that in the third generation, type *WWCC* has increased greatly in

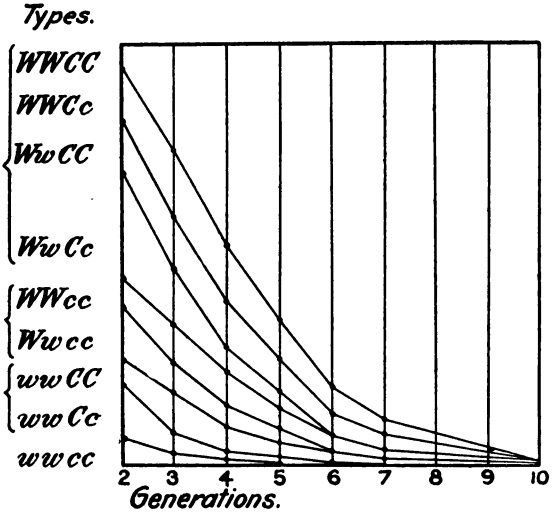

FIG. 5.—Graphic illustration of ten generations of a hybrid in a self-fertilized species selected for type *WWCC*. The letters and spaces between curves have the same significance as in figure 4.

proportion. Type *WWCc* about holds its own until the fourth generation, after which it decreases. The same is true of type *WwCC*, but type *WwCc* decreases rapidly from the second generation onward. At the end of ten generations practically the whole population is of type *WWCC*, which is pure winter club wheat, with a very small admixture of other types. This shows the effect of mass selection after hybridization in the case of self-fertilized crops. The result is a much more rapid approach to the one type selected than occurs in the corresponding case with cross-fertilized crops as shown in figure 3.

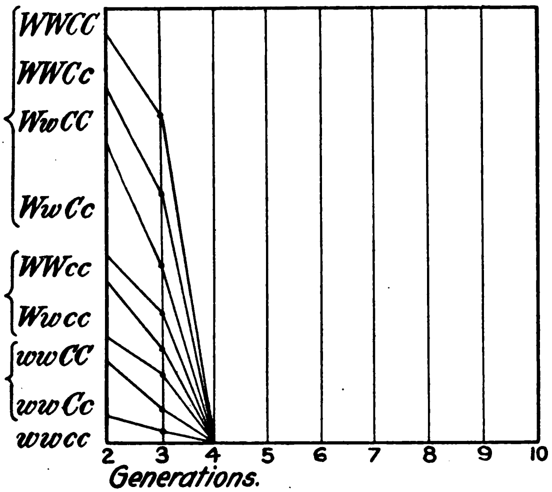

FIG. 6.—Graphic illustration of the effect ot individual selection in a self-fertilized species on progeny of the hybrid *Ww Cc*. After the third generation the race is pure for the selected characters (both dominant in this case). The letters and spaces between curves have the same significance as in figure 4.

The effect of individual selection, i. e., selection in which the seed of the individuals selected is kept separate, is shown for self-fertilized crops in figure 6. In this figure, as in the preceding, the space beginning opposite each type symbol shows the proportion of that type from generation to generation. In this method of selection we save each second-generation individual which appears to be of type *WWCC*. This includes all plants of types *WWCC*, *WWCc*, *WwCC*, and *WwCc*. The seed of each plant is kept separate. In the next generation we save seed only from those rows or plots in which there has been no splitting up. This gives us at once the type *WWCC* in pure and fixed form. This is shown in figure 6, where the space representing type *WWCC* occupies the whole diagram beyond the third generation.

CROSS-FERTILIZED SPECIES.

The problem of utilizing hybridization in the production of new forms in cross-fertilized species which are propagated from seed is somewhat complicated by the fact that the individuals to be used in crossing may themselves be heterozygote for many characters. Diversity in such species differs from that in self-fertilized species in this respect: In the latter we usually have in homozygote form all the combinations possible of the characters found in the group, while in cross-fertilized species we have the same combinations, but not in homozygote form. In self-fertilized species, when a desired combination is not at hand, we can easily produce it and get it in fixed form. In cross-fertilized species, if the desired combination is not at hand, we can get it by crossing, but can not be sure of keeping it unless it is a form that can be propagated vegetatively, such as berries, tree fruits, and potatoes. The best we can do in cross-fertilized species which are propagated from seed is to make a cross with a view to getting a certain desired combination of characters and then select the desired type until we get a fairly constant strain of it. The results that follow such selection have already been explained under the head of "Cross-fertilized species," page 36, and illustrated in figure 3.

It has already been hinted that in cross-fertilized species we should not try for too great uniformity, as such uniformity in cross-fertilized species usually goes with weak development. If by crossing and subsequent selection we can get two forms, each of which is homozygote for the same desirable characters but heterozygote for other characters which are of no importance, and then plant them so that the two forms will cross freely, we shall probably have the nearest approach to the desired end attainable in such forms.

MENDELIAN ANALYSIS OF HETEROZYGOTE RACES.

When an individual which is heterozygote for a given pair of allelomorphs is self-pollinated it breaks up in the next generation into three forms, or types, two homozygote and one heterozygote. Let our pair of allelomorphs be represented by Aa. With self-pollination we have in the next generation one-fourth AA, one-half Aa, and one-fourth aa. That is, one-fourth of the seed produced is homozygote for A, one-fourth for a, and one-half of it is heterozygote, Aa. Hence, in such species as apples, pears, strawberries, and cassava, which do not ordinarily reproduce true to seed because they are heterozygote, usually for many of their characters, if we self-pollinate them, in the next generation we get many forms that are homozygote for some characters. If the species will endure continued self-pollination it is clear that we could in eight or ten generations break up any variety of this kind into homozygote types that would reproduce true to seed. In fact, there are a good many varieties of some of the species just mentioned that do reproduce practically true from seed. The Royal Anne cherry of Oregon and Washington is a case in point. Many of its seedlings can hardly be distinguished from the original variety. Where it is possible to secure these homozygote forms by this process of breaking up into pure races, a process which we may call Mendelian analysis, such forms might be of great importance to the breeder. They might render possible the deliberate combination of highly desirable characteristics existing in different varieties. Some very interesting work of this kind has been done. Prof. S. M. Tracy, working under the direction of the writer, has thus obtained three races of cassava which reproduce practically true to seed. They are now being used in an attempt to propagate this crop from seed instead of from cuttings. If the attempt is successful, and it promises to be so, it will permit a considerable extension of cassava culture into latitudes in which it is not practicable to propagate cassava from cuttings, because of the difficulty of keeping the cuttings over winter.

In Volume V of the Annual Reports of the American Breeders' Association, Dr. W. T. Macoun, of Canada, reports some very interesting facts regarding the seedlings of the Wealthy apple. There was probably some cross-pollination in this case, but the seedlings give very plain evidence of the parentage of this important variety of apple. This is an important and nearly virgin field of investigation, and more work of this kind will be looked for with interest.

HETEROZYGOTE CHARACTERS.

In some crosses, or hybrids, characters appear in the first generation of the cross that were not apparent in either parent. These characters may belong to either of two classes. First, they may be due to the heterozygote nature of the hybrid. Characters of this class can be taken advantage of by the breeder only when the plant concerned can be propagated vegetatively. In crops propagated from seed a character which is due to the heterozygote nature of the plant which bears it will appear in the next generation in only half the progeny. Such characters can not be fixed by selection; at least no one has as yet succeeded in doing so, and it is highly improbable that it can be done.

The most common type of such characters is the well-known vegetative vigor seen in many hybrids. It is not unusual in sorghum fields to see here and there a stalk which is much larger and taller than the rest of the field. Investigation has shown that these plants are hybrids. The writer has noticed in his work with hybrid wheat that the first-generation hybrid is much more vigorous and stronger growing than either of the parents as a rule, though this vigor in hybrid wheats is not so marked as it is in sorghum. In corn it is especially marked. Dr. G. H. Shull by the close breeding of two varieties secured practically homozygote strains of them, which were then crossed. The yield of the hybrid was about five times that of the attenuated self-fertilized pure strains. It should be remarked that the pure strains of corn, because of the close inbreeding, had become very weak yielders, while the hybrid yielded an exceedingly large crop.

Dr. E. M. East, of the Connecticut Agricultural Experiment Station, in a similar manner produced on small plots at the experiment station yields of corn exceeding 200 bushels per acre from hybrid seed. Here is an important point for the corn breeder.

A good deal of effort has been made to secure uniformity of the ears in corn by a system of rather close breeding. This method will give the desired uniformity, but the close breeding in a species naturally cross-fertilized is likely to lead to lessened yields. Is it not better to breed for excellence, taking care not to breed too closely, and let uniformity take care of itself? A method of using two strains of corn in the breeding plot in order to secure hybrid seeds for the field crop has already been described.

Increased vegetative vigor does not occur in all crosses. Before recommending the cross-breeding of any particular crop in order to secure increased vigor, the fact that in that crop the desired results will follow should be determined.

The following are other cases of characters which occur only in heterozygote form. In the cross between Black Andalusian fowls and a variety of White Andalusians having black splashes on the feathers, here called White Andalusians for convenience, the heterozygote is blue. If these blue fowls be mated with each other one-fourth of their progeny is black, one-half blue, and one-fourth white. If Blue Andalusians are desired, 100 per cent of blues can be obtained only by mating blacks and whites.

According to Professor Bateson, exactly the same phenomenon occurs in the Bredas, a breed of fowls found in Holland.

A similar case occurs in the cross between a certain red primrose and a certain white primrose, reported by Professor Bateson. The heterozygote is purple and is known to the trade under the name of "Imperial Primrose." Fifteen years of persistent selection has failed to cause this primrose to come true to seed. Every year one-fourth of its seed produce plants having red flowers, one-half of the seed produce plants having purple flowers, while the remaining one-fourth have white flowers.

Dr. G. H. Shull found a mottled character in the seed coat of certain first-generation hybrid beans which proved to be a heterozygote character; that is, when it appeared it was always heterozygote and would then reappear in only half of the plants whose seeds were mottled. Prof. R. A. Emerson, of the University of Nebraska, found the same character in beans, as did also Professor von Tschermak, of Vienna, and Mr. Locke, of Ceylon.

Cases like those cited seem to be due to the presence of two characters in different varieties which are not manifest in those varieties; but when brought together by hybridization they react on each other in some unknown manner so as to give rise to a new character. At the same time they form a Mendelian pair and separate again on the formation of gametes. Perhaps in such cases two chromosomes, which meet to form a bivalent in the reduction division, each throw off into the cell a different chemical substance, and these two substances, by reacting on each other, give rise to the new character. When these two chromosomes are not together in the same cell the character does not appear.

Most of such characters are probably reversions to lost characters. The fact that there are mottled races of beans like those produced by Shull and others, and which reproduce true to seed, is in favor of this suggestion. In these mottled beans which reproduce true to type we may suppose that each of the chromosomes in question produces both of the chemical substances which we have supposed give rise to the character. If this is the case, then nonmottled varieties of three types could arise from a mottled variety by the loss on the part of the chromosomes producing the two necessary substances of the power of producing one or the other or both of these substances. If in one variety of beans one of these substances and in another variety the other substance is missing, crossing the two varieties would cause the lost character to reappear. This matter will be considered more fully when we are considering the subject of latency of hereditary characters.

Thus far we have considered only those new characters arising in crosses and which appear only in heterozygote form. There is a second class of characters arising in crosses that may be fixed by proper procedure. In working with gillyflowers Bateson and his coworkers found an interesting case of this kind, which will be considered more fully under the head of latency and need only be referred to briefly here. In crossing a certain white variety with a cream-colored variety the progeny produced red flowers, and in the second generation some individuals were obtained having red flowers and reproducing true to seed. Evidently this result was due to the fact that two characters neither of which produced any effect when alone but when brought together gave rise to a visible character did not form a Mendelian pair and could consequently both be transmitted together.

The reason why a character of this type can be fixed is seen in the following. We have assumed that the new character arises by the bringing together of two other characters that are not allelomorphic to each other; that is, do not form a pair which must separate on the formation of gametes. If we call one of these characters *A*, its absence *a*, the other *B*, and its absence *b*, the first-generation hybrid is constituted thus, *AaBb*. This hybrid produces four types of gametes, namely, *AB*, *Ab*, *aB*, *ab*. An ovule of the type *AB* uniting with pollen of the type *AB* gives *AABB*, a homozygote strain in which the new character is fixed. While such cases as this are not common, they may occasionally represent important advances in breeding. It is therefore well for the breeder to understand them. Several such cases have been found. They also probably represent reversions to lost characters, at least in most cases.

Characters may also appear in the second generation of a hybrid that were not apparent either in the first generation or in either of the parents. This is especially the case when a character is hypostatic in one of the original parents of the cross; that is, when it is covered up or hidden by some other character. A case in point is the appearance of brown beans in the second generation of the cross between black and white, reported by Shull. Here the brown is hypostatic to black, i. e., obscured or hidden by the black, in the black parent. Letting *B* represent black, *b* its absence, *D* brown, and *d* the absence of brown, the formulæ for the black and white forms and the hybrid between them is—

Black, *BBDD*.
White, *bbdd*.
Hybrid, *BbDd*.

The gametes produced by this hybrid are *BD*, *Bd*, *bD*, and *bd*. The union of an ovule of the type *bD* with pollen of the same type gives *bbDD*, a brown type.

Similar cases are known in animals.

POSSIBILITY OF ENTIRELY NEW CHARACTERS.

While most apparently new characters that arise in crossing are probably reversions to lost characters, it is easily conceivable that entirely new characters might arise in this manner. It seems probable that some cases of reversion are due to reaction between chemical substances, one of which is derived from one parent and the other from the other. These substances are probably produced in the cells of the respective pure strains before the cross; but they produce no effect because they are not both present in the same cells. It is conceivable that in some races there may have occurred evolutionary changes that result in considerable modification of the chemical contents of the cells but which produce no visible effect on external characters. In two related races these evolutionary changes may be quite different, and when we cross two strains that have been separated for some thousands of generations we may get, by reactions between substances that in the respective pure races are of no effect, entirely new characters which thus seem to appear suddenly, but which in reality may have been thousands of years in developing. Characters arising in this way would appear only in heterozygotes if the two factors brought together happened to form a pair. But if they did not form a pair the new character would be capable of being fixed.

Some phenomena have occurred, especially in crosses between distinct species, which probably belong in the class here considered, though not enough work has been done in this direction to make this entirely certain.

RECIPROCAL CROSSES.

If in one cross we use the pollen of race *A* on the stigmas of race *B*, while in another cross we use the pollen of race *B* on the stigmas of race *A*, these two crosses are said to be reciprocal to each other. Ordinarily such crosses give identical results. In his work with hybrid wheats at the Washington Agricultural Experiment Station the writer made reciprocal crosses in three instances, and in each case the results of the reciprocal crosses were identical. There are cases, however, where reciprocal crosses give different results. In some species the plant produces more than one kind of pollen and only one kind of ovule, as Correns found in Bryonia. He crossed a diœcious species with a monœcious species. When he used pollen of the diœcious species the hybrids were male and female in equal numbers, but when he used the pollen of the monœcious species the hybrids were all female. A number of other cases are known which may be explained on a somewhat similar basis. In a few cases differences have appeared in reciprocal crosses for which no explanation has been found. The plant breeder should make a careful record of any such cases coming under his observation, as they may lead to important advances in our knowledge of the principles of heredity.

EVOLUTIONARY CHANGES AND THEIR RELATION TO PLANT BREEDING.

While a great deal of study has been given to the general subject of evolution, actual knowledge of how and why evolutionary changes occur is very limited. The discussion this subject has received has been largely theoretical, and usually in support of some theory as to the manner in which such changes occur.

We may perhaps distinguish two or more classes of evolutionary changes. A complex organism is provided with many hereditary characters—that is, characters which appear in successive generations. These characters may change in the manner of expression. For instance, a species having purple flowers may change with reference to the shade of coloring, or a variety may change in size, and so on. Again, a character may become latent, possibly lost entirely. Thus, a purple-flowered species by the loss or latency of a factor for purple, may become red. Again, a red flower might become purple by the revival of the latent factor for purple.

It is probably safe to say that most evolutionary changes are of the classes mentioned in the preceding paragraph. Take, for instance, the color of wild mammals. Nearly all mammals, so far as they have been studied, have the same factors for color. The differences in the colors of the different species have come about simply by modifications in these same factors. Yet, some evolutionary changes result in the development of new characters. Beards on grasses must at one time have been new organs. But changes of this kind are comparatively rare, and occur so seldom that we can take little cognizance of them in practical breeding work.

As stated before, we do not know the cause of these changes. One school of biologists maintains that evolutionary changes are slow and gradual, another that they take place by instantaneous steps, which may be large or small—that is, that they are "discontinuous." We are more interested here in the amount of change that may occur in a given time than in the manner in which such changes take place. The important point is that when evolutionary changes do occur they are usually permanent changes, and the new forms resulting are subject to the laws of selection and hybridization which have already been outlined. That these permanent changes do occur can not be questioned. That in general they are merely changes in hereditary characters already present is equally certain. Doctor Nilsson in his work with the cereals at Svalöf has many times taken an unselected lot of seed from a standard variety of field grain and found it in the main to consist of a large number of fixed types differing from each other in various ways. When the same character is studied throughout the numerous strains that occur in a field it is found to present nearly every possible gradation in different strains, but generally speaking in each of the strains the gradation found is fixed.

Jennings, in his study of Paramecium, found in wild cultures almost an indefinite number of strains, each differing permanently in size, and these differences undoubtedly are due to permanent changes of hereditary characters, as in the case of Nilsson's cereals. Jennings's investigations indicate that there might be found in Paramecium almost every gradation in size, but that the size of each particular strain is fixed.

The principal relation of these changes to the work of the plant breeder lies in the fact that a crop as grown under field conditions will usually consist of a large number of strains which differ from each other on account of evolutionary changes which have occurred in the past, and the breeder can by selection secure the strains which are of greatest value.

A few instances are known in which important changes have been brought about by persistent selection. De Vries, by continued selection from a 13-rayed strain of *Chrysanthemum segetum,* was finally able to produce a double-flowered variety. Burbank found a single specimen of California poppy which had a scarlet line on one of its petals. By persistent selection from this plant he was able to get a scarlet poppy. Cases of this kind are not understood, yet they are important from the standpoint of the breeder. They show that we have much yet to learn in this important field. It may be stated that scarlet-flowered California poppies occasionally occur in nature. This fact shows that at least part of the species has the scarlet color factor. It is probable, therefore, that Burbank started with a plant having this factor, and by selection merely eliminated other color factors.

PLACE EFFECT.

It is a well-known fact that when a crop is moved to a locality which is radically different from that in which it was previously grown it sometimes behaves in a surprising manner, presenting unlooked-for variations. This subject has not been studied nearly as much as it ought to be. We really do not know the behavior of the variations which occur under such conditions, because so little attention has been given to them.

Take, for instance, the case of the tomato in southern climates. Some of the standard varieties of tomatoes present very peculiar modifications when seed grown in the North is planted in the far South. The first year the fruit is normal and resembles the fruit that would have been produced in the North; but if seed of the southern-grown fruit be saved and planted, the next year the fruit is of a very different character and remains so from generation to generation under the new conditions. The writer is informed by Mr. W. W. Tracy, sr., of this Bureau, that when the seed of these transformed tomatoes is taken back to the North and planted, while the first year it grows the southern type of tomato, the next year it reverts to its northern form. Cases of this kind are well worth more attention than they have received.

It is to be noted that in the case of the tomato just referred to the same change occurs in all the individuals. In this connection, some work recently done by Dr. Albert Mann, of this Bureau, is of special interest. Although the results are as yet unpublished Doctor Mann kindly permits me to refer to them.

Three years ago he obtained from Doctor Nilsson, of Svalöf, a number of the pedigreed or pure-line strains of barley grown at that station. Seed of five or more of these were sent to thirty-eight localities throughout the country in 1907, representing nearly two hundred tests. In all cases more or less transformation occurred in each of the strains under investigation. Generally speaking, every individual of a given strain went through identically the same transformation in the same locality. The results obtained the second year on some thirty locations indicate that the changes made by these plants are permanent as long as they are grown under the new conditions.

In several instances it was found that a given strain did not behave alike, part undergoing one modification and part another. A careful study of one of these cases revealed the fact that one end of the plot was on sandy soil and the other on loam and that all the plants at the same end had suffered the same change.

Doctor Mann has called my attention to the important fact that these changes suffered by pure lines when taken to a radically different environment from that to which they had been accustomed seem in no way to be adaptive changes. They are apparently not adjustments to the new conditions, but are changes caused by the new conditions. Apparently, they may be advantageous or disadvantageous to the plant under its new surroundings.

It is easily seen that by studying this question with types of plants from which all other kinds of variation have been eliminated, results of fundamental importance may be obtained. The conclusions, which are at least indicated by the very meager data at hand, are that these new-place effects produce similar results on similar individuals, that they are permanent under the changed conditions, and that they are fortuitous in character. It is by no means established, however, that these conclusions are general. This is evidently an important and nearly virgin field for investigation.

NON-MENDELIAN CHARACTERS.

The only case known to the writer of a non-Mendelian character which has been clearly made out and for which the method of inheritance has been determined is one recently published by Dr. Erwin Baur, of Berlin, and which relates to the method of inheritance of the white margin of certain leaves.[a] The white-margined plants produce only pollen and ovules carrying the white tissue character. But when these plants are crossed with ordinary green plants the new individual thus formed is capable of producing both kinds of tissue. It would appear that in the cross-fertilized ovule, part of the cytoplasm of the cell carries the tendency to develop green tissue and part the tendency to develop white tissue. If at any cell division one of the daughter cells should happen to receive only cytoplasm of a certain kind then the tissue descended from that daughter cell will be either pure white or pure green, as the case may be. Plants originating from this cross between white and green are thus called mosaics. A leaf or bud originating on the line of contact between the tissues will be white on one side and green on the other. If it originates wholly from white tissue it will be pure white; if wholly from green tissue it will be pure green. Occasionally, however, the white tissue on the stem of such plants may extend as a thin surface layer over the green tissue. A bud coming through such a layer will be composed of green tissue within and a thin layer of white tissue without, and this bud gives rise, by division and propagation, to a new white-margined plant.

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[a] Since the above was written the publication of Castle's monograph on inheritance in the rabbit has been made by the Carnegie Institution. Had this publication appeared earlier it would have received extended notice in these pages.

Another case which should be mentioned here is that of the inheritance of ear length in rabbits studied by Prof. W. E. Castle, of Harvard. The cross between long-eared and short-eared rabbits had ears intermediate in length, and their progeny were like the hybrid in this respect. In this case the mechanism of inheritance is not clear; and it is barely possible that it is simply a very complex case of Mendelian inheritance.

In a great many crosses between very distinct species we do not get strictly Mendelian phenomena and we do not know exactly why. It is highly probable, however, in the writer's opinion, that the reason is to be sought in the following. Most of the organs and parts of an organism are developed as the result of the interaction of a good many factors which are Mendelian in nature. For instance, the development of horn tissue in cattle may be the result of the interaction of three or four or even more chemical substances arising from different organs in the cell. Now, if in two races of cattle we find a difference in only one of these chemical substances, then the differences between the two races would behave as a simple Mendelian character; but if there were differences in all the substances concerned we should have an exceedingly complex case of Mendelian inheritance, the unraveling of which would require such large numbers of progeny from hybrids that it would be practically impossible to determine the nature of the inheritance in the case. The writer is of the opinion that the lack of simple Mendelian characters in species hybrids is partly of the nature here outlined. In some species crosses apparently wide departures from Mendelian principles occur. Take, for instance, the cross made by Burbank, resulting in the Primus berry. Here there was wide diversity in the first-generation hybrids. The one first-generation individual from which the Primus berry is descended was unlike any of the others. But this individual has reproduced true to seed from the beginning.

Rosenberg has shown that in a similar case in the genus Hieracium the first-generation hybrids, which are not alike, have different numbers of chromosomes. Presumably, in such cases, the chromosomes of the two species crossed differ so much in habit that they can not function together properly, and some of them are lost in the early cell divisions of the young hybrid. In some individuals, one chromosome is lost, in others other chromosomes are lost; so that, if the supposition here made is true, the young first-generation hybrids do not have the same complement of hereditary characters, which would account for their not being alike.

The fact that these hybrids do not split up in Mendelian fashion in the second and later generations suggests that the corresponding chromosomes in the two sets of chromosomes brought together in these wide crosses are so unlike that they are not drawn together to form bivalents in the reduction division. That is, the reduction division does not occur in the mother cells which produce ovules and pollen. If this should prove to be true, then either of two alternative courses of events would give hybrids which reproduce true to seed without Mendelian splitting.

(1) Seed may be produced parthenogenetically, without the intervention of a reduction division and subsequent fertilization, and this asexual production of seed may continue from generation to generation.

(2) Without a reduction division in the first-generation hybrid, a pollen nucleus may unite with an ovule nucleus, thus giving a nucleus having two sets of chromosomes like the one possessed by the first-generation hybrid. The set of chromosomes in the first-generation hybrid is presumably composed of chromosomes part of which are from one species and part from the other. The double nucleus thus formed will have two sets of chromosomes, every one in one set having an exact duplicate in the other. After this, that is, in the second and later generations, reproduction would take place in the usual manner, without any Mendelian splitting, for the two halves of each bivalent formed in the reduction division would be exactly alike.

It would probably be possible, by cytological study of these constant hybrids, to determine whether the absence of Mendelian splitting is due to either of the causes above suggested.

MUTATIONS.

The term "mutation" has been used and is now used in so many senses that a great deal of confusion has arisen in consequence. Prof. Hugo De Vries, of Holland, after investigating some hundreds of species of plants, found one species (*Oenothera lamarckiana*) which occasionally produced offspring that were unlike the parent. Some of the new individuals were capable of reproduction true to type. These forms he called mutations. The work of Dr. R. R. Gates, of the University of Chicago, who is making a careful study of the chromosome behavior in these mutants, indicates strongly that these mutations are due to accidents occurring in the reduction division by which chromosomes are either lost or gained or exchanged, so that some of the daughter cells are provided with a set of chromosomes differing from that of the parent species. A good deal of work must yet be done before this matter is settled, and until we know more about it we can not assign mutations of this class to their proper place in heredity and in evolutionary progress.

The term "mutation" has also been applied to any permanent evolutionary change of whatever magnitude or whatever its cause. It is hardly probable that all evolutionary changes are due to accidents in cell division. It would seem rather that most of such changes are due to permanent changes in whatever material is responsible for the development of hereditary characters, and it is probable that we shall ultimately have to make a distinction between these two types of so-called mutations.

LATENCY.

Characters sometimes fail to develop, although present. The reason for such failure may fall into any one of several categories. One of the most important recent papers dealing with this phase of the subject is that of Dr. G. H. Shull in the American Naturalist, Volume XLII, July, 1908. The following classification of the different types of latency follows, in the main, Doctor Shull's paper, departures therefrom being noted in the text.

I.—LATENCY DUE TO SEPARATION.

Bateson and his coworkers crossed a cream-colored strain of gillyflowers with a white strain and secured a hybrid which had red flowers. This is explained by assuming that in the cross two characters are brought together which when separated are incapable of producing red flower color, but which when together give rise to this color. Many other breeders have found similar instances, and these characters, which when alone produce no visible effect but when in the presence of other characters give rise to visible manifestations, have been called "cryptomeres" by Prof. E. von Tschermak, a term which is derived from the Greek and which etymologically means "hidden parts." Both von Tschermak and Bateson have shown that purple color in gillyflowers is due to three such cryptomeres. Two of these without the third give rise to the red color. When the third is present with the first two purple arises. There are other cryptomeres present in gillyflowers which modify these colors, but the numerical relations in their transmission have not yet been fully made out.

Shull found a cryptomeric character in beans in a cross between certain brownish-seeded beans and white-seeded beans. It appears that the white variety carried a cryptomere which when present with the factor which gives rise to the brown color converts the brown into black, thus giving in the hybrid a character which was apparently absent in both of its parents.

In this case we may represent the formula of the two parents as follows:

White parent = *BBpp*.
Brown parent = *bbPP*.

Here *B* stands for the cryptomere which converts the brown color into black (and which is latent in the absence of *P*) and *P* for the producer of the brown pigment. The hybrid would have the formula *BbPp*. The second generation of this hybrid would be as follows:

	B.	*P.*	*pb.*
1 *BBPP*	1		
2 *BBPp*	2		
1 *BBpp*			1
2 *BbPP*	2		
4 *BbPp*	4		
2 *Bbpp*			2
1 *bbPP*		1	
2 *bbPp*		2	
1 *bbpp*			1
16	9	3	4

The first column in the above table gives the nine types in the second generation of the hybrid, and the figures at the left of the formula show the relative frequency of the types. Thus type *BBPP* constitutes one-sixteenth of the second generation, type *BBPp* two-sixteenths, and so on. Since *B* and *P* are both present in types *BBPP*, *BBPp*, *BbPP*, and *BbPp*, these four types, constituting together nine-sixteenths of the second generation, will all be black. Types *bbPP* and *bbPp* are brown, while types *BBpp*, *Bbpp*, and *bbpp* will all be white, although two of them have the factor *B*. The factor *B* has no effect in the absence of *P*. We thus have in the second generation of this hybrid 9 blacks, to 3 browns, to 4 whites.

A more complex case of this kind is that of the purple gillyflowers already mentioned. In this case we have to deal with the following factors:

C=one factor of red.
R=other factor of red.
P=the factor for purple.

Of these factors *C* and *R* are cryptomeric to each other; that is, neither of them produces a visible effect except in the presence of the other. *P* is cryptomeric to both *C* and *R*. The factor *P* was first discovered by crossing a cream-colored variety carrying the factor *C* and a white variety carrying the factors *R* and *P*. The first-generation hybrid was therefore *CcRrPp*. The second generation of this cross gave the following:

	P.	R.	W. (or cream).
1 *CCRRPP*	1		
2 *CCRRPp*	2		
1 *CCRRpp*		1	
2 *CCRrPP*	2		
4 *CCRrPp*	4		
2 *CCRrpp*		2	
1 *CCrrPP*			1
2 *CCrrPp*			2
1 *CCrrpp*			1
2 *CcRRPP*	2		
4 *CcRRPp*	4		
2 *CcRRpp*		2	
4 *CcRrPP*	4		
8 *CcRrPp*	8		
4 *CcRrpp*		4	
2 *CcrrPP*			2
4 *CcrrPp*			4
2 *Ccrrpp*			2
1 *ccRRPP*			1
2 *ccRRPp*			2
1 *ccRRpp*			1
2 *ccRrPP*			2
4 *ccRrPp*			4
2 *ccRrpp*			2
1 *ccrrPP*			1
2 *ccrrPp*			2
1 *ccrrpp*			1
64	27	9	28

This gives in the second generation 27 purples, 9 reds, and 28 whites or creams.

The above illustrations will give the reader an idea of the behavior of cryptomeric characters. These characters are not infrequent, and in the early days when such cases arose they were frequently reported as "exceptions to Mendel's law." Their inheritance is now well understood.

II.—LATENCY DUE TO DOMINANCE OF ABSENCE OVER PRESENCE.

Latency due to dominance of absence over presence was not separately considered by Shull in the paper referred to. Generally speaking, the presence of a character is dominant to its absence, but there are some exceptions. Two of the best known relate to horns in cattle and beards in wheat. We do not know exactly why these characters do not develop when they are in the heterozygote state. It is possible that in both these cases the absence of horns or beards may be due to the presence of some inhibiting factor, in which case the present category of latency would be a simple case of dominance of presence over absence. It seems probable, however, that these characters are simply unable to develop unless represented by two allelomorphs. The reasons for this assumption are rather too abstruse to be given here, for to make them clear would require a great deal of space, and they are also more or less speculative at the present time.[a]

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[a] See article by Shull in American Naturalist for July, 1909.

III.—LATENCY DUE TO HOMOZYGOSIS.

This group of facts might perhaps be better described as "patency due to heterozygosis." It includes those cases where a character is patent only in heterozygotes. The following discussion differs in some details from that given by Shull.

In Shull's bean crosses, mottled first-generation hybrids occurred between varieties neither of which was mottled, and subsequent investigation showed that the mottling only occurred in heterozygotes. Tschermak and Locke have both reported similar cases; also Professor Emerson, of the University of Nebraska. In all these cases the mottled beans produce progeny half of which is mottled and the other half not, thus giving a departure from the usual 3:1 ratio found in ordinary Mendelian characters.

The following explanation of all the above cases is here offered. The explanation will be given for mottled character, from which the explanation of the other cases may be easily inferred. The fact that in beans there are mottled varieties which breed true and which when crossed with the new type of mottled beans give ordinary Mendelian phenomena greatly strengthens the hypothesis here stated. Let us suppose that originally the mottling was due to two correlated characters; that is, to two characters which are always transmitted together. We may represent the determiner for this double character as M^a_c. The formula for those strains of mottled beans which reproduce true to type would then be $M^a_cM^a_c$. If we suppose that in some strains of these mottled beans the character *a* becomes latent or is lost, while in other strains the character *c* does likewise, while in still others both *a* and *c* become latent, we get three types of nonmottled beans, the formulæ for which are M^aM^a, M_cM_c, and MM. A cross between the first and second of these nonmottled types would give mottling of the character found by Shull. This cross would have the formula M^aM_c. In the next generation this would split up into one-fourth M^aM^a, one-half M^aM_c, and one-fourth M_cM_c, in which only the heterozygotes would be mottled, for it is only in them that we have both factors of the mottling. Either of the three types of nonmottled beans crossed with permanently mottled beans would give the ordinary Mendelian behavior of the mottled character in which in the second generation we should have three mottled to one nonmottled.

This same explanation is in accord with the facts in the case of the blue color in Andalusian fowls and the purple color in Imperial primroses. In the case of the blue Andalusians the blue may not be a reversion to a lost character, but may be, in a sense, a new character; but on the above explanation its presence in heterozygotes is assumed to be explicable on exactly the same basis as the presence of mottling in those beans in which it occurs only in heterozygotes.

IV.—LATENCY DUE TO HYPOSTASIS (MASKING).

Sometimes a character may be hidden by the presence of another character which simply obscures it. Thus, in the hair of most species of mammals there are both yellow and black pigments, each of which may be visible because of a certain other factor which causes them to develop more or less in different regions of the same hair. But in the absence of this controlling factor the black and yellow pigments develop in the same regions of the hair and the black thus obscures the yellow. Prof. T. H. Morgan found a case in the cross between the black rat and the Alexandrian rat, in which the black color was dominant over the gray color of the Alexandrian rat, presumably because the black color hid the other color characters.

Characters which are thus obscured by the presence of another character are said to be latent by hypostasis—that is, they are hypostatic to the obscuring character, while the latter is said to be epistatic to the obscured character. These convenient terms were suggested by Professor Bateson. In one of his crosses between black beans and yellow beans Shull obtained some seal-brown beans, and inferred that the seal-brown had been present in the black beans, but was there obscured by hypostasis.

V.—LATENCY DUE TO INHIBITION.

The category of latency due to inhibition is much like the last and was included by Shull, perhaps properly, with it. It seems possible, however, that it may deserve separate treatment. In the cases considered characters have been invisible simply because some other character present obscured them. There are cases, however, where the presence of one character seems to prevent the development of another character. For instance, Prof. V. L. Kellogg, of Leland Stanford Junior University, in crossing certain white and certain colored varieties of silkworms found the white to be dominant. Similar phenomena have been found by Bateson and Davenport in poultry, and the writer, in cooperation with Mr. Q. I. Simpson, has found the same in swine. Here the presence of the white character seems to prevent the color from developing rather than simply to obscure the color. Perhaps we might not be justified in treating this case as anything else than hypostasis. At any rate, the behavior in inheritance is exactly as in the case of hypostasis, as far as the ratios of the various types are concerned.

VI.—LATENCY DUE TO FLUCTUATION.

Some Mendelian characters are highly variable. Shull cites the case of certain leaf lobings which vary greatly under unfavorable conditions, and sometimes entirely fail to develop. When the plants in question were grown under favorable conditions, it was easy to demonstrate that leaf lobings are a good Mendelian character, but under certain unfavorable conditions the lobing disappears, thus confusing the Mendelian results. Kellogg found a similar case in silkworms. Certain strains of silkworms which produce salmon-colored cocoons when crossed with certain white strains gave results which showed clearly that the salmon color is a Mendelian character. But in some crosses the salmon color became extremely variable, extending all the way from almost pure white to very deep salmon color, thus somewhat obscuring the numerical relations of the colors in the second generation of the hybrid. In some of Correns's work with variegated plants he found a similar character. The variegation, although a good Mendelian character, varied with true green leaves as one extreme, and in some crosses this fact made the number of green leaves in the second generation larger than theory called for.

CORRELATION.

A good many cases have been found where two characters which, so far as appearance goes, are not physiologically related to each other seem always to be transmitted together, and the breeder frequently gets irregular results because of this coupling or correlation of characters. For instance, Tschermak found in Chinese oats that hull-less seed is correlated with long, many-flowered spikelets, and that these two characters were always transmitted together. In Price and Drinkard's work with tomatoes at the Virginia Agricultural Experiment Station they found what seems to be a case of this kind. In one of their crosses one of the parents had green foliage and two-celled fruit. The other parent had yellowish green foliage and many-celled fruit. The hybrid was like the first parent. In the second generation of this hybrid all the plants having green foliage had two-celled fruits, and all those having yellowish green foliage had many-celled fruits, thus indicating that the many-celled condition of the fruit is transmitted with the yellowish green leaf character, at least in this case. Hedrick and Booth, in their work with tomato hybrids, found that dwarf stature was correlated with dark-green rugous leaves, while standard stature was similarly correlated with lighter green smooth leaves.

Such cases sometimes give the breeder a good deal of difficulty. They are of special importance in relation to theories of heredity, and should always be carefully noted and reported.

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U. S. DEPARTMENT OF AGRICULTURE,

BUREAU OF PLANT INDUSTRY—BULLETIN NO. 166.

B. T. GALLOWAY, *Chief of Bureau.*

THE MISTLETOE PEST IN THE SOUTHWEST.

BY

WILLIAM L. BRAY,

SPECIAL AGENT, INVESTIGATIONS IN FOREST PATHOLOGY

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Forestry
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3-15-1930

LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., September 24, 1909.

Sir: I have the honor to transmit herewith a paper entitled "The Mistletoe Pest in the Southwest," by Prof. William L. Bray, formerly a special agent in the Office of Investigations in Forest Pathology.

The paper embodies the results of several years of investigation of the various phases of the mistletoe pest and an account of the methods of combating it that are known at present. The subject of control of the mistletoe pest is still under investigation in this Bureau. This paper, however, marks the completion of Professor Bray's work on the subject. I recommend that it be published as Bulletin No. 166 of the special series of this Bureau.

Respectfully,

A. F. Woods,
Acting Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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B. P. I.—515.

THE MISTLETOE PEST IN THE SOUTHWEST.

INTRODUCTION.

The name "mistletoe" was long ago applied to the mysterious parasitic European shrub to which, centuries later, Linnæus gave the technical name *Viscum album*, by which name it is at present distinguished from other related species also called mistletoe. These other more or less closely related species have been discovered from time to time in almost all parts of the world—certainly in most of the warm countries—until at the present time a large kinship circle or family of mistletoes is known, embracing more than 600 species. In the course of botanical explorations in the Western Hemisphere numerous representatives of this family were found, and among them one which so closely resembled the original mistletoe that it was given the generic name Viscum, with the specific designation flavescens; indeed, one early botanical explorer, Thomas Walter, called specimens found in the Carolinas *Viscum album*, under the impression that they were identical with the European plant. Later, the pioneer botanist, Nuttall, suggested that the American plant differed from the European one widely enough to deserve separate generic distinction, and so proposed the name *Phoradendron* (tree thief). The name then became *Phoradendron flavescens*. Interestingly enough, the specimen upon which this name was based was from Texas.

In spite of the fact that there are some scores of species of mistletoe in the Americas (including the West Indies), this *Phoradendron flavescens* enjoys the distinction of being *the* American mistletoe, and has been accepted in this country in lieu of the genuine mistletoe of Europe and invested with much of its traditional and historical setting.

DISTRIBUTION AND HARMFUL OCCURRENCE OF MISTLETOE.

The American mistletoe is a leafy, green, parasitic shrub, commonly found growing upon various species of broad-leaved trees throughout the Southern States and extending in more or less modified forms across Texas, southern New Mexico, and Arizona to southern California, and thence northward in the coast region to

Oregon and Washington. Eastward its northern limit is in New Jersey, southern Pennsylvania, southern Ohio, Indiana, Illinois, Missouri, and eastern Oklahoma. Speaking generally, mistletoe is held in rather high regard everywhere because of its inherently interesting mode of life, because of the traditional and historical atmosphere which invests the original mistletoe of Europe, and because of its desirability, for the above and other reasons, as a decorative Christmas shrub. The fact that it is a parasite implies a possible injury to the tree upon which it grows, but, again speaking generally, the injury is regarded as relatively slight and more than offset by the feeling of regard for the parasite. Among people who see it rarely, and, especially among those living in northern cities who purchase small sprigs or bunches of it at a good price for Christmas decoration, the idea of mistletoe being a harmful parasite upon trees is quite lost sight of. Nevertheless, there are localities in which mistletoe becomes so abundant upon trees and so harmful to them as to make the control of it or its extermination a serious practical question.

This is notably the case in parts of Texas. Between the ninety-sixth and ninety-seventh meridians in Texas is a belt of country in which mistletoe is a serious parasite in many localities. The area most harmfully infected would be comprised in a circle of 100 miles, more or less, in radius, having its center at Austin. The north-south extension of this area is really greater than its east-west dimensions, for to the eastward one passes presently into the more humid and more heavily timbered country, and westward the available hosts for the parasite become fewer.

The climatic conditions of this area have a more or less direct bearing upon the question. Between the ninety-sixth and ninety-seventh meridians in Texas and Oklahoma lies a zone of transition from the humid climate of the Gulf States to the arid climate of the Southwest. The heavy forest growth of the South does not enter this belt, except as it follows the moist soils of river and creek bottoms, and even in these favorable situations the luxuriant growth becomes checked by the decreasing rainfall and drier atmosphere. Upland tree growth is stunted; the trees occur more sparsely, are broader of crown, less tall, and more frequently of imperfect growth. The trees bear evidence of a struggle against unfavorable conditions. In this region it becomes a difficult matter to secure umbrageous trees for shading and beautifying streets and parks and private grounds. Not many native species are suitable for these purposes. Very little has been done toward the solution of the whole question of selection, planting, and care of shade trees.

In spite of the less inviting conditions for forest growth, mistletoe appears to flourish better in this belt than elsewhere; at least, it is relatively more abundant than it is eastward. It is a curious fact, whose explanation is not very obvious, that mistletoe is more varied in form and relatively more abundant in the arid districts of the Southwest (e. g., portions of New Mexico and southern California) than it is in the Gulf States east of the ninety-sixth meridian. It is not that the growth of mistletoe as a shrub is more vigorous than in the eastern belt; as a matter of fact, in the more humid climate it makes a most luxuriant and symmetrical growth, but fewer of the trees relatively are infected and these evidently in more restricted localities.[a] In river or creek bottoms or in swamps one sees the taller trees with bunches of mistletoe far up on the remote branches. In middle Texas, on the contrary, mistletoe is by no means confined to bottom-land trees, but it infests those of upland prairies also. Stunted native growths and transplanted trees are especially apt to be infected, and not merely by isolated bunches of mistletoe on remote branches, but throughout the tree on old as well as young branches, and not infrequently upon the main trunk itself, so that the whole tree is infected, weakened and disfigured, and finally killed. (Pl. I, fig. 1.) Thus it comes about that just in the region where trees in perfection are especially difficult to find they are more than elsewhere subject to harmful infection by this parasite. The explanation may be suggested that mistletoe, like a good many other plants of arid situations, requires much sunlight for its best growth and especially for the development of flowers, and thereby of numerous and vigorous seeds, and is at a disadvantage in competing with the heavy shade-casting foliage of forests in humid climates. The necessity for light might explain why in bottom-land forests of the East mistletoe is confined to the highest branches of the tallest trees (as shown by observations made in the case of bottom-land timber in parts of Arkansas, southeastern Oklahoma, and northeastern Texas), and how with increasing intensity of sunlight and the more meager foliage and open stand of trees incident to the drier climate of the Southwest mistletoe is enabled to spread over the entire tree.

That more arid environmental conditions have acted in the nature of a stimulus to mistletoe in its growth and reproduction may be alleged from the fact that in the arid Southwest there is much more variation in the habit of the plant than there is in the Atlantic and Gulf forest regions. Thus between middle Texas and southern California there are several distinct types or varieties of *Phoradendron flavescens* (*macrophyllum*, *villosum*, *orbiculatum*, and *pubescens*), besides several more distinct species, notably *Phoradendron californi-*

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[a] Exceptions to this statement are not unusual. Thus, at Houston, Tex., at various points in Louisiana, and also in some localities in Mississippi and Tennessee, mistletoe has been reported as harmfully abundant in isolated trees or clumps of trees in dooryards and parks.

cum, which infests many species of desert trees and shrubs, and *Phoradendron bolleanum* and *P. juniperum*, which last two are especially noteworthy as being parasitic upon coniferous trees, especially desert junipers.

BIOLOGY AND LIFE HISTORY.

A brief account of the life history and of the habits of nutrition of mistletoe will assist in making clear the reason for its harmfulness to trees. The plant is a parasite. It fastens itself upon its host, the tree, penetrates its tissues, and draws nourishment from it, deforming it and sapping its vitality. Yet the mistletoe is a green, leafy plant; that is, it possesses the pigment chlorophyll, which gives the green color to normal vegetation. Some of the tropical species of mistletoe bear leaves as large as those of an American elm. The presence of green leaves indicates that the mistletoe has the power, which independent green plants everywhere possess, of constructing organic foodstuffs, such as starch, out of inorganic compounds (carbon dioxid and water), utilizing sunlight as the source of energy in the process. It is therefore only partly a parasite so far as dependence upon a host for food is concerned, but apparently none the less harmful on that account. It secures from its host apparently only what the normal, shrubby plant derives from the soil, namely, water and certain necessary mineral constituents. Imagine a grapevine or trumpet creeper, while retaining its foliage, to sever connection with the soil and to thrust root-like outgrowths into the body of the tree to which it clings, in order to absorb from the tree what before it absorbed from the soil. This would represent the relation which mistletoe sustains to its host.

In this connection it is instructive to observe that the mistletoe family, viewed as a whole, shows a progressive development of parasitism. Thus at one end of the series stands the Australian genus Nuytsia, whose single species is a nonparasitic tree. At the opposite extreme is the degenerate, absolute parasite *Phrygilanthus aphyllus*, parasitic upon a cactus of the genus Cereus in Chile. This plant is said to possess neither cotyledons nor foliage leaves, nor does it develop the vigorous shrubby habit characteristic of mistletoes generally. The more familiar mistletoes are sometimes called "half parasites," but they also show great variation in habit from the very broad-leaved forms above mentioned down to those which are yellow-green and quite leafless; e. g., *Phoradendron juniperum* and *Arceuthobium pusillum*, the latter of which barely emerges from its host.

In the general sequence of events the life history of mistletoe is just like that of any flowering woody plant; for example, the hackberry, upon which it preys. It bears flowers; in due time the berries follow, each with its inclosed seed; the berries are deposited by birds or beaten down by rains upon the branches, where under favorable conditions the seeds germinate, and if the seedling becomes established upon the branch it grows again to the age of producing flowers and seed, and so on from generation to generation. Of course the mistletoe seed is more limited than the hackberry in its choice of a substratum upon which to grow, since the only situation in which it has any prospect of developing a plant is upon some part of a living tree.

DEVELOPMENT OF FLOWERS AND FRUIT.

The flowers of the American mistletoe are minute and inconspicuous, although in some tropical mistletoes they are relatively large and showy. The flowering season in Texas falls usually in December, which is approximately the date of flowering for the species throughout its range. The plant is diœcious; that is, any one individual is wholly male or wholly female. Manifestly some plants never produce berries. This separateness of pollen-producing and ovule-producing plants makes it a matter of importance whether female and male plants grow in close proximity and whether there are any special means by which pollination is effected. Several of the conspicuous-flowered tropical mistletoes are regularly pollinated by insects. It is claimed also that the European mistletoe (*Viscum album*) is pollinated by insects, but so far as has been determined the American mistletoe apparently depends upon the wind to carry its pollen.

After the flowering period and pollination, the development of seed and berry goes forward very slowly. With the approach of the following winter the berry begins to enlarge and by December the seeds are ripe and the berries pulpy and white. Thus it happens that the flowering season of this year coincides with the ripening of fruits begun a year ago.

DISTRIBUTION OF SEED BY BIRDS AND OTHERWISE.

The seed when ripe is inclosed in a clear, sticky pulp covered by a tough, semitransparent skin, the whole constituting the mistletoe berry.[a] This pulp appears to be in some degree an object of food to certain birds, notably to mocking birds, cedar birds or waxwings, and to robins in Texas,[b] and the seeds are distributed in considerable numbers by these birds either in their excrement or by being wiped from the beak against a branch in the birds' efforts to remove the adhesive pulp. In either case the pulp still remaining about the seed causes it to stick to the branch and by drying to become firmly pasted there. It is the conclusion of most observers that the mocking bird is the chief distributer of mistletoe seed, but perhaps the cedar birds actually distribute more, for in March and April these birds appear in flocks of hundreds in search of berry mast—especially hackberries—and during the brief visits of a few days or a week or two all the berry-laden trees are visited repeatedly until the berries are gone. During these flights, mistletoe berries are also eaten, though probably not much noticed until the hackberry crop is exhausted. Robins also are reported to be common distributers of mistletoe seed. In the vicinity of Austin large flocks of robins spend the winter, or part of it, in the cedar brakes, where they feed largely on cedar mast; but at times they appear in numbers about farmyards and in towns, feeding upon hackberries, and during these visits also upon mistletoe berries.

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[a] In the case of the European mistletoe the sticky pulp of the berry is utilized in the preparation of bird lime.

[b] Doubtless most berry-eating birds feed more or less upon mistletoe berries, according to the abundance or scarcity of other, choicer kinds. Thus in Bulletin No. 120 of the University of Texas on the American mistletoe, page 7, Mr. York reports that sparrows and cardinals are the principal birds, next to the mocking birds, which feed upon mistletoe berries.

Mistletoe is, however, not wholly dependent upon birds for the distribution of its seeds, for as the spring advances and the berries grow softer they fall away easily, becoming crushed and adhering to the branch below. Especially are they beaten off in heavy downpours of rain and washed against the branches, where they are left adhering in favorable situations for germination. The character of infection of certain cedar elm trees illustrates very plainly this method of infection. Pendent branches become laden with bunches of mistletoe from base to tip, showing how the seeds were washed down the branch during a heavy rainfall.

STRUCTURE AND VITALITY OF THE SEED.

Of course, mistletoe seeds become planted in the ways just described in all sorts of places and in favorable weather are induced to germinate in almost any situation—upon branches, upon the main trunk, upon leaves, dead twigs, fences, and even upon mistletoe itself—but the only situation in which there is any prospect of this germination resulting in the establishment of a mistletoe plant is, as previously stated, upon the living branch or trunk of a tree, and only then where the bark is thin or cleft, or otherwise in a condition to permit the penetration of the root axis or sinker of the seedling. In any event, the bark or epidermis of a tree would seem to be barren soil, since it dries so quickly. This is particularly true in central Texas and westward, where the atmosphere is habitually dry. The seeds have need to be strongly drought resistant, and this quality they seem to possess in a marked degree.

They begin to be distributed upon branches in December and January, but favorable conditions for germination are not likely to occur before March, and perhaps not before April or May, depending upon the temperature, and when this is sufficiently high upon the appearance of a period of rainy, humid weather. Whether the seeds placed upon branches in midwinter remain capable of germination as late as April or May is not known, but of course many berries remain to be distributed as late as May. If it be true that birds eat mistletoe berries only when other choicer kinds are no longer available, then the chief season of distribution would about coincide with the more favorable conditions for germination.

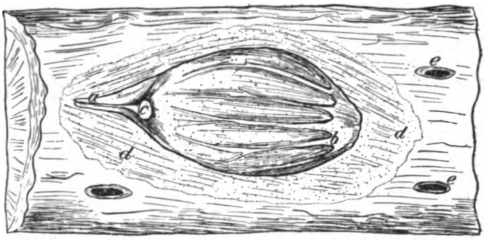

Fig. 1.—A seed of mistletoe pasted on a branch by berry pulp and ready to germinate: *a*, Beak of seed coat; *b*, fibrous coat of seed; *c*, root tip of embryo; *d*, *d*, berry pulp; *e*, *e*, lenticels on branch. (All very much enlarged.)

The pulpy covering in which seeds are embedded upon a branch is a protection to them against extreme drying out and doubtless useful also in absorbing water before germination, thus allowing the seed to lie in a moist, slimy matrix. (See fig. 1.) The seed structure proper is also adapted to the arid conditions upon a branch. The seed is invested in a fibrous coat (endocarp) quite unlike the customary hard shell of berry seeds, which is peculiarly active in absorbing water and transmitting it to the living parts within. The peculiar thickening of the walls of the cells in this fibrous coat suggests the water-absorbing tracheid cells of sphagnum moss and of the velamen in the air roots of certain orchids, both of which types are noteworthy because of their water-absorbing properties.

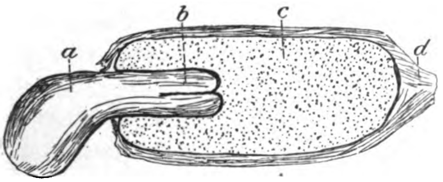

Fig. 2.—Sectional view of a germinating mistletoe seed: *a*, Embryo, showing knob-like enlargement of root end; *b*, cotyledons of embryo; *c*, endosperm or food supply; *d*, fibrous seed coat.

Within the fibrous coat lies a body of food material or endosperm in which the minute embryo lies embedded, except for its slightly protruding root tip (fig. 2). Both embryo and endosperm retain chlorophyll pigment throughout the dormant period, but previous to germination the green color becomes intensified and the presence of a gas (oxygen?) in the interspaces shows that the seed is already a carbon-assimilating body, able to proceed with its development within the moment of arrival of favorable conditions or of lying dormant and uninjured with the return of arid conditions. It appears capable of repeating this behavior of alternate activity and dormancy throughout the germination period and until the seedling is fully established, and therefore less influenced by sudden fluctuations of moisture and dryness. In short, the seed in its germination phase is a well-adapted drought plant or xerophyte.

GERMINATION AND ESTABLISHMENT OF THE SEEDLING.

The first apparent movement in germination consists in the elongation of the axis (hypocotyl) of the embryo, whereby the root tip is thrust beyond the beak of the seed jacket, thus becoming directly exposed to the air and sunlight. Upon becoming exposed the axis bends so as to bring the blunt end of it into contact with the underlying branch. This prompt bending in its growth appears to indicate a sensitiveness of the tip toward the branch, but it has been shown that it is on account of its sensitiveness to light that the axis bends, and the bending has for its object the avoidance of too intense illumination. This, however, results in bringing the root tip of the embryo against the branch. The root end of the embryo is blunt or even knob-shaped while still within the seed jacket, and as it emerges and turns toward the branch the end further enlarges until it becomes prominently knob-formed even before it comes into contact with any underlying object (fig. 2). When, however, it touches the branch, the knob becomes broader and is flattened on the contact side, as when a plastic object is pressed firmly against a hard surface. Thus it behaves like an adhering disk or sucker, such as one observes in the Boston ivy, where the tips of the clinging tendrils flatten against the wall. At the center of the flattened disk the cells continue to push forward, with the result that a point of tissue, the primary sinker, bores its way, or, perhaps more accurately, dissolves its way, into the tissues of the branch (fig. 3), for the cells of this puncturing point are able to secrete a substance (enzyme) capable of dissolving the walls of cells lying in its path. Thus it really dissolves and absorbs the tissue of the host. This primary sinker pushes downward through the soft bark zone (cortex, phloem, and cambium) until it reaches the younger wood cells. Meanwhile an axial strand of cells in the primary sinker becomes differentiated into water-transporting tracheids,

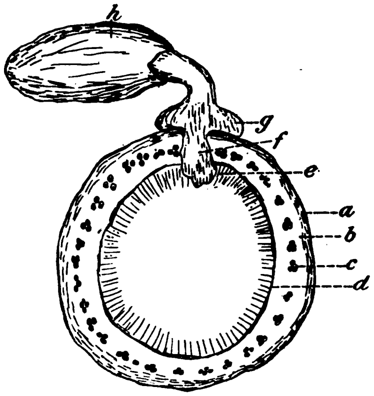

FIG. 3.—Diagram showing the method of penetrating a branch by a mistletoe seedling: *a*, Corky covering of branch; *b*, cortex zone; *c*, bast fibers; *d*, cambium or growth ring; *e*, wood zone; *f*, sinker of mistletoe penetrating to wood zone; *g*, disk; *h*, body of mistletoe seed.

of which those formed in the wood zone of the host become applied to the water-carrying cells of the host, thus establishing an efficient means of conducting water and mineral nutrients from the host into the parasite. The mistletoe seedling is now virtually a tiny bud graft (fig. 3).

Having thus established its connection with the source of some of its food supply, the upper end of the hypocotyl with the minute cotyledons gradually withdraws from the inclosing and partly digested endosperm, and becoming erect the cotyledons slowly expand as the first pair of green leaves. Perhaps this is as far as development goes during the first season. In some species of mistletoe the cotyledons remain covered by the seed jacket and endosperm (if there is any) during all of the first season. Apparently the progress of development at this period depends upon weather conditions. In a dry climate these are apt to be such as to interrupt repeatedly the progress of germination and of becoming established. Existence becomes largely a question of endurance during this period, and it is probable that in a season of unusual warmth and humidity the seedling progresses in its development farther than merely to expand the cotyledons; whereas, in an unfavorable season, if the seedling survives at all it may approach the winter with germination, in the popular sense, still incomplete. This seems to be a reasonable interpretation of facts and conditions thus far observed in the field, and it points with renewed emphasis to the peculiarly resistant qualities of the mistletoe at this period of its existence. In spite of these qualities, however, the great majority of mistletoe seedlings perish, or the seeds never germinate at all in the face of such extreme arid conditions as frequently prevail.

It should be noted that the mistletoe in establishing itself as previously described, with its primary sinker in contact with the wood cells, has the problem of adjusting itself to the season's growth in thickness. This it does by maintaining a zone of embryonic tissue in the sinker corresponding to the cambium zone of the host.

Some time after the seedling has established itself as described, probably not until the second season's growth, there arise from the primary sinker in the zone of soft bark, or cortex, lateral outgrowths called cortical roots, or cortical haustoria, which spread along and around the host stem in this cortex zone, extending farther and farther from the original point of penetration (fig. 4). At intervals from the side of the cortical roots nearest the wood zone more sinkers arise and penetrate along the line of least resistance (medullary rays) into the wood, where they develop a connection with the water-carrying vessels as the primary sinker did. These cortical roots persist and increase in thickness; indeed, it appears to be the thickening of these at their junction with the parent axis which gives the enlarging mistletoe bush its strongly buttressed attachment to the branch (fig. 4). The presence of these persistent cortical roots interrupts the formation of host tissue exterior to them, and thus they come to lie more or less exposed along the surface of the branch. At these exposed places (possibly also from the younger cortical roots still within the cortex zone) adventitious buds are developed which may give rise to new mistletoe shoots. (See figs. 5 and 6.) They do this in considerable numbers if from any cause the original mistletoe plant is injured, or especially if it be broken off, as is most frequently done when the effort is made to rid a tree of the parasite. In this way the cortical roots are stimulated to further growth and to giving rise to repeated crops of mistletoe shoots. Scraping off the old plants stimulates the development of more adventitious buds and thus tends to enlarge the area of infection.

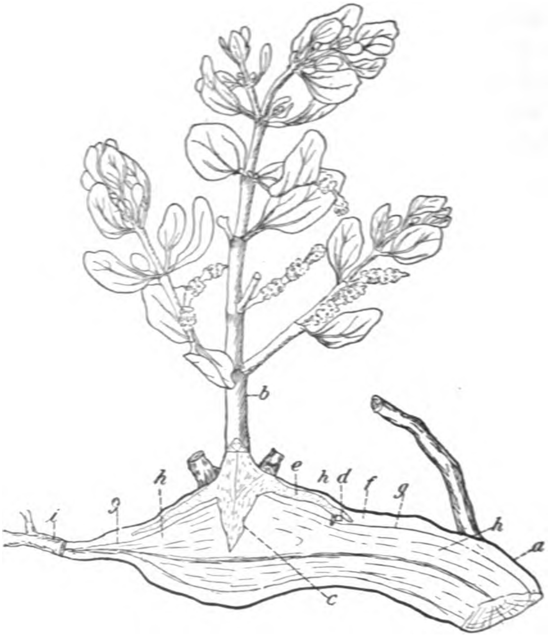

FIG. 4.—Sectional view, partly diagrammatic, of a branch infected with mistletoe, showing the relation between parasite and host: *a*, Branch of host tree; *b*, mistletoe; *c*, primary sinker; *d*, sinker from cortical root *e*; *f*, cortex or soft bark; *g*, cambium or growth ring; *h*, wood of branch. The starving and dwarfing of the branch beyond the mistletoe is shown at *i*.

It has been observed that in some trees, or at least in some situations on the branch, there is no considerable spread of cortical roots and no development of shoots from adventitious buds. Thus, in the case of the water oak one may find huge bushes of mistletoe a yard in diameter on branches eight or ten years old with not a single indication of the spread of the infection along the branch. This may be observed also in the mesquite and doubtless in any other tree where the primary mistletoe plant started on a very young branch and has developed unharmed. (See fig. 5.) In the course of time, however, the original plant is destroyed by some agency or other, but the cortical roots persist and thenceforth develop secondary shoots from adventitious buds. In this way may be explained the characteristic occurrence of mistletoe on old branches and even on trunks, as shown not infrequently on mesquite and very commonly on hackberry. The cortical haustoria have persisted for years, in many cases producing an unsightly deformity of the branch or trunk (fig. 7). There is an obvious similarity between this behavior of mistletoe and that of certain noxious weeds, such as Johnson grass, where from an original plant underground rootstocks spread in all directions, sending down more roots into the soil and sending up plant after plant into the air until a wide area is beset by it; also in the further respect that merely cutting off the tops only serves to stimulate the underground parts to greater activity in spreading and breaking out in new places.

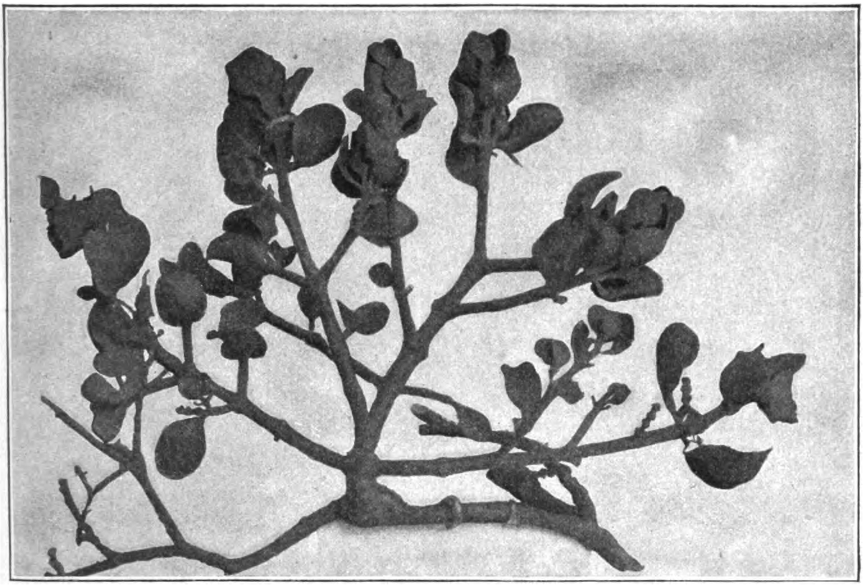

FIG. 5.—Mistletoe on a branch of a cedar elm tree, showing the starved end of the branch and how mistletoe comes to be terminal on a branch.

RATE OF GROWTH.

During the period in which the parasite is becoming established the rate of development, as already shown, is extremely slow. During the whole of the first season the mistletoe plant may not grow more than a quarter or half inch in length. After becoming thoroughly established, however, growth is relatively rapid, depending, as does the host also, upon the character of the season. The shoots from adventitious buds have been observed to grow to the length of 4 to 6 inches in a single season following the spring pruning of the previously developed crop of shoots. In the case of water oaks growing in wet bottom-land soil, bunches of mistletoe have been observed to develop in six to eight years into a shrub having a spread of nearly 3 feet and to be more than an inch in diameter just above the buttressed point of attachment to the slender branch of the host (Pl. II, fig. 1). The rate of growth varies with the host, being much slower in the cases of the mesquite and the osage orange. The location of the host with respect to moist or dry soils naturally also affects the rate of growth of the parasite.

LONGEVITY.

The parts of mistletoe embedded in the tissues of its host appear to have no fixed limit to continued existence except the death of its host. Specific data in this connection are not at hand for the American mistletoe, but in the case of European mistletoe Tubeuf states that often sinkers are found extending through sixty to seventy annual rings of growth. There are many cases in Texas where mistletoe has been repeatedly broken from large branches during the past twenty or twenty-five years. In cases where the trunk of the mesquite and the hackberry are notably deformed it is probable that the infection is nearly as old as the host.

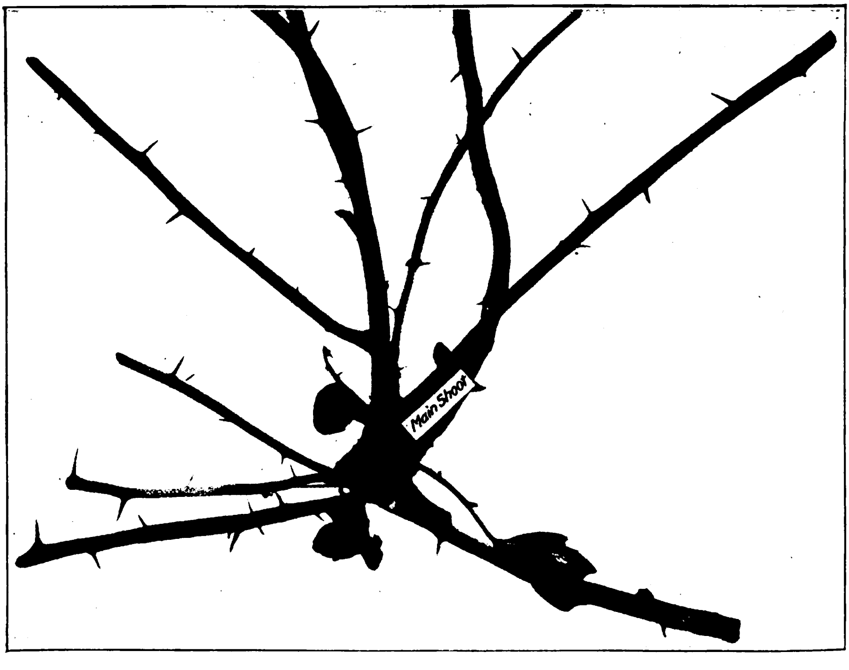

Fig. 6.—A branch of an Osage orange tree infected with mistletoe, showing deformity and multiplication of branches at the point of infection.

With regard to the aerial part it would appear that any single bush would scarcely survive more than eight or ten years, chiefly because of the likelihood of its being broken off by storms, or being killed by freezing, or otherwise being mechanically destroyed. It is maintained that in extreme cold weather mistletoe has been largely killed out over large areas; for example, in the unprecedented cold wave of February, 1900. Its own bulkiness and brittleness would seem to operate toward the self-destruction of the mistletoe bush. In the case of infection upon the mesquite, spoken of elsewhere, the parasite so injures the branch upon which it sits as to kill the branch and thereby destroy itself. Usually, however, accident to the aerial part of the parasite merely results in stimulating the development of adventitious buds—and thereby in multiplying the number of mistletoe shoots upon a gradually widening area of infection.

EFFECT UPON THE HOST.

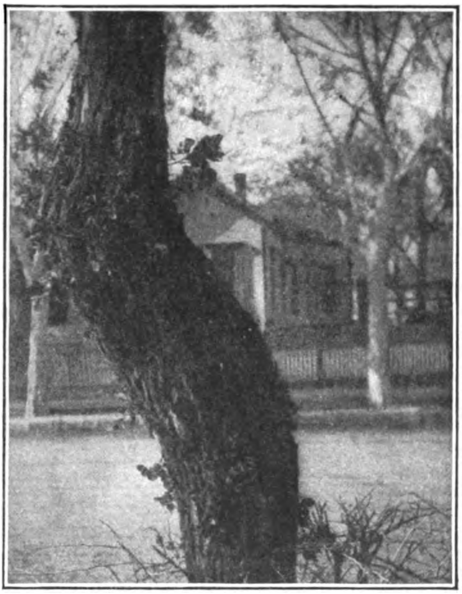

FIG. 7.—The trunk of a mesquite tree at Waco, Tex., deformed by long-standing mistletoe infection.

Perhaps in the majority of cases the original point of infection is upon a small, remote branch. The habit of the mistletoe is of course to draw sustenance from the branch and in increasing quantity as the parasite increases in size. The immediate result is to starve that portion of the branch lying beyond the point of infection, and while this part may persist for some years alive without noticeable growth, in the end it dies, and the mistletoe thus comes to occupy the end of the branch. (See fig. 5.) This habit is particularly well shown in the water oak, where very large clusters 2 to 3 feet in diameter swing from the end of a long slender branch not more than an inch in diameter next the swollen point of junction of the host and parasite (Pl. II, fig. 1). At the point of attachment also the branch is stimulated to excessive growth, which gives rise to deformities of varying shapes on different host species. In the water oak just mentioned both branch and mistletoe are enlarged like a clumsy piece of welding. Frequently, as in the Osage orange, the branch is stimulated to an excessive formation of shoots, forming a sort of witches' broom. (See fig. 6 and Pl. II, fig. 2.) Large branches, and not infrequently the main trunks of trees, may be greatly deformed by the mistletoe. This happens where infection occurred when the tree was young and has persisted to misshape all its subsequent growth. (See fig. 7.) On the other hand, very many trees are infected for years without showing any noteworthy deformity, and, as a matter of fact, this item is not one of serious economic importance.

Mistletoe not only causes mechanical injury, but it saps the vitality of the branch and when sufficiently abundant often the whole tree; and in the case of the hackberry, especially, often results in the death of the entire tree. About Austin considerable numbers of hackberry trees have been and are being destroyed in this way. At Bryan, Tex., this is true of water oaks. It has been supposed that perhaps the mistletoe merely supplants the end of the branch which was starved by its presence, and that while it receives what the branch would otherwise receive, it in turn contributes to the tree by its assimilating activity what the displaced branch would have done. This seems never to be the case at any time, and it is certain that when the majority of branches become so supplanted by the mistletoe, the tree dies, showing the parasite to be always a drain upon its host. One of the curious results of infection has been often observed, especially in the Uvalde region, where bunches of mistletoe on remote branches of the mesquite, becoming large, so injure the branch that it decays beneath the mistletoe, which thus itself is starved and killed and presently falls away, leaving the branch free from infection. This is probably due to decay induced by the starving of the branch beyond the original point of infection.

THE POINT OF ATTACK.

In the process of establishing itself upon the host, the critical point for the mistletoe seedling is to penetrate the covering of the branch so as to reach the food-supplying cells of the cortex and wood. The sinker can exert pressure and is doubtless able to force an entrance through fissures or through natural openings, such as lenticels, and between bud scales, as shown by Cannon.[a]

The growing tip of the sinker has been shown to secrete an enzyme capable of dissolving the walls of certain cells lying in its path. Whether heavily cutinized walls or the walls of dead cork cells can be dissolved by this secretion has not been fully determined. Cork and bark certainly offer much more resistance to the forward growth of the sinker than cellulose walls do, and it is quite unlikely that a heavy layer of these could ever be penetrated by a mistletoe sinker. When infection begins on the old parts of a tree it must be at some fissure or thin place in the bark. Naturally the younger branches, and especially twigs of last season's growth, present the most vulnerable points of attack, and as therefore would be expected, infection begins in the majority of cases on the remote young branches, where the protective covering is thinner and the lenticels (breathing pores) still numerous. Here also the buds offer a point of attack. Cannon states that in the case of a mesquite branch he has seen as many as a half dozen successive buds bearing mistletoe. The hypocotyl of the seedling pushes its way between bud scales to the more easily penetrated tissue at their base. Cannon also holds that even on the youngest branches the penetration of a sinker is conditioned upon its finding a lenticel or inserting itself between bud scales; but in view of the abundance and varying aspects of infection it seems necessary to ascribe a more active rôle to the sinker than that of mechanically pushing its way through openings and crevices, and that a less haphazard mode of infection prevails. However, no actual proof is at hand that the sinker can secrete an enzyme that will dissolve cutinized or cork cell walls.

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[a] Cannon, W. A. Observations on the Germination of Phoradendron villosum and P. californicum. Bulletin, Torrey Botanical Club, vol. 31, pp. 435–443. 1904.

The location of the point of infection upon a tree appears also to have some relation to the perching habits of the birds which eat the berries. This idea is held notably in the case of mocking birds. Large areas of mesquite-covered country to the westward of San Antonio show a predominance of cases where a single plant of mistletoe occupies the most conspicuous spot upon the tree, namely, near the apex of the farthest spreading top branch. This appears to coincide with the choice of perching places by the bird in its flight from tree to tree. The habits of cedar birds in their repeated short flights and perching during their spring visits in search of berry mast are also such as to afford the largest likelihood of mistletoe seed being deposited on the youngest branches.

TREES MOST SUSCEPTIBLE TO MISTLETOE INFECTION.

It is a question whether any tree is wholly immune to attacks from mistletoe. Certainly there is reason to believe that mistletoe could be induced to grow upon any living woody plant. But from the actual status of infection in any community where mistletoe grows there are some trees which are practically immune. One of the curious things about the matter is the prevalence of infection upon different species in different localities. Thus, in the vicinity of Austin, the hackberry and the cedar elm are the trees most frequently and heavily infected. The sycamore, though common in central Texas, both native and cultivated, has not been reported to have mistletoe in any case; whereas in the river bottoms of Arkansas and southeastern Oklahoma it is one of the most commonly infected trees. Broad-leaved elms are practically immune in the Austin region, but at Muskogee, Okla., and northward such elms are as thoroughly beset with mistletoe as the cedar elm is at Austin. At San Antonio and southwestward the mesquite is the chief mistletoe host. At Bryan, which lies farther within the humid belt, the water oak is the most infected species. At Marble Falls, about equally distant but westward from Austin, the live oak and mesquite are reported as the main hosts. So in the osage orange belt of northeastern Texas—notably from Greenville to Paris—that species (*Toxylon pomiferum*) is more infected than others. In the vicinity of Calvert, Tex., the blackjack oak (*Quercus marilandica*) is abundantly infected, but other species not notably so. In reality, the species most infected in all these instances are either the most abundant or else the most prominent in certain situations; for example, along water courses or about farmyards and in towns. Even so, it is not clear why, for instance, the blackjack oak, which is the prevailing host in certain districts, should be comparatively immune in another district where mistletoe is even more common. Extending the range of observation, it is found that the dominant host for *Phoradendron flavescens* and its different forms varies with the geographical location, as follows: In the South, the water oak and other red or black oaks of wet soils, gums, elms, and sycamores; in the Santa Clara Valley, California, especially on deciduous oaks (the prevailing form here being *Phoradendron flavescens villosum*); in southern California *Phoradendron flavescens macrophyllum* on the poplar, willow, ash, and others; at Tucson, Ariz., *Phoradendron flavescens macrophyllum* on the poplar (cottonwood), ash, and black locust, and *Phoradendron flavescens villosum* on oaks and the hackberry.

LIST OF HOSTS OF THE MISTLETOE IN TEXAS.

Pecan (*Hicoria pecan* (Marsh.) Britton).
Hickory (*Hicoria* species). (At Columbus, Tex.)
Post oak (*Quercus minor* (Marsh.) Sargent).
Bur oak (*Quercus macrocarpa* Michx.).
Texan oak (*Quercus texana* Buckl.).
Water oak (*Quercus nigra* L.).
Willow oak (*Quercus phellos* L.).
Blackjack (*Quercus marilandica* Muench.).
Live oak (*Quercus virginiana* Mill.); (Marble Falls and Comanche, Tex.; not noted at Austin).
Cedar elm (*Ulmus crassifolia* Nutt.).
White elm or American elm (*Ulmus americana* L.).
Hackberry or Sugarberry (*Celtis mississippiensis* Bosc., and varieties).
Osage orange (*Toxylon pomiferum* Raf.).
Paper mulberry (*Papyrus papyrifera* (L.) Kuntze).
Sassafras (*Sassafras sassafras* (L.) Karsten).
Sweet gum (*Liquidambar styraciflua* L.).
Apple (cultivated varieties).
Pear (cultivated varieties).
Cherry (*Prunus* species, wild).

Thorn (*Crataegus* species).
Roemer's acacia (*Acacia roemeriana* Scheele).
Mesquite (*Prosopsis juliflora glandulosa* (Torr.) Sargent).
Water locust (*Gleditsia aquatica* Marsh.).
Honey locust (*Gleditsia triacanthos* L.).
Prickly ash (*Xanthoxylum clava-herculis* L.).
China (*Melia azedarach* L.).
Wild China (*Sapindus marginatus* Willd.).
Black gum (*Nyssa sylvatica* Marsh.).
Persimmon (*Diospyros virginiana* L.).
Water ash (*Fraxinus caroliniana* Miller).
Berlandier ash (*Fraxinus berlandieriana* A. de C.).

To this list must be added the interesting case of a climbing vine (*Tecoma radicans* (L.) Juss.) as a host plant observed at Bryan, Tex.

No doubt this list might be very much extended by a careful survey throughout the State.

FREEDOM OF INTERCHANGE OF HOSTS.

The question arises as to whether parasitism in the mistletoe is in any considerable degree exclusive, i. e., whether by continued growth on a given host species it becomes less capable of infecting a different species. A survey of the field outside of the *Phoradendron flavescens* circle shows that this sort of thing is possible, at least within certain limits. Thus there is a group of species brought together under the generic name Arceuthobium, all of them being parasitic exclusively upon coniferous trees, and some of them upon one species exclusively. More to the point is the case of the European mistletoe (*Viscum album*) and its circle of related forms. Tubeuf[a] distinguishes three forms: (1) That infecting broad-leaved trees, Laubholz mistel; (2) one which infects fir trees (*Abies pectinata* and *A. cephalonica*), Tannen mistel; and (3) the form parasitic on pines (*Pinus sylvestris* and *P. laricio*), Föhren mistel. Tubeuf maintains that none of these three forms is capable of infecting hosts of the others, and has sustained his position by abundant observations in the forest and by inoculation experiments.

It should be noted here that in the case just cited the form which is parasitic upon broad-leaved trees has numerous hosts—twenty-two host species are listed for a single park forest—and that a good deal of freedom of interchange among hosts is possible. It seems likely, therefore, that the central Texas form of mistletoe may be more or less easily established upon all of the hosts (at least in any given district) by seed carried from the mistletoe growing upon any one of them, and that the immunity which some trees seem to have is due to the mechanical hindrance exercised by the bark or cork, or the simple epidermis, to penetration by the primary sinker, or possibly to the density of shade, as in the case of the China tree (*Melia azedarach*).[b] This relative immunity of species becomes, however, a matter of practical importance as indicating one of the qualities (resistance to mistletoe) that will influence the choice of trees for planting for shade or wind-break or ornament.

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[a] C. Tubeuf. Die Mistel (Viscum album) Pflanzenpathologische Wandtafeln no. 1 (text), 1906, and more recently in Naturwissenschaftliche Zeitschrift für Land und Forstwirtschaft, no. 5, vol. 7, 1907.

Further, it should be noted that the mistletoe varies considerably in habit on different hosts, and especially where the hosts occupy notably different situations as to soil and climate, being in this respect plastic, like the majority of plants capable of existing in widely different soil and climatic conditions. Probably the qualities acquired in any given situation are not such as to forbid a gradual or even ready tolerance for other conditions.

LOCATION OF INFECTED TREES.

Speaking generally, mistletoe-infected trees are those which occupy moist soils, namely, in river bottoms and along creeks and ravines leading to the uplands. In the South generally, certain swamp-inhabiting trees (gums and water oaks) are notably mistletoe hosts. There is no doubt a reason for this in the more or less constant demand which the mistletoe makes on its host for water. In the central Texas mistletoe belt this preference of mistletoe for trees of moist situations is obvious, but it is by no means limited to trees of such locations. Quite on the contrary, the most noteworthy and destructive instances of infection are on isolated trees or clumps of trees in dooryards or parks and along streets and highways. There is a notable preference for isolated trees. Even in timbered bottom lands the heavily infected trees are those which stand out conspicuously in or about a field or clearing. (Pl. I, figs. 1 and 2; Pl. II, fig. 1.) In close stands of timber the average tree seems much less likely to be infected than the same species in the open. Those which are infected in heavy stands are the trees which overtop their neighbors. Perhaps the need of mistletoe for abundant sunlight explains in part its absence in close forests and the predominance of it in exposed trees. This fact is of the greatest consequence in the present consideration, for while the loss to forest trees in a close stand is negligible, the concentrated attack of mistletoe on isolated trees is a blow on a vital spot, for the maintenance of adequate shade trees is a difficult matter, quite apart from the rôle played by mistletoe.

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[b] One correspondent states that mistletoe has been observed to grow upon China trees in southern Texas.

A further item of significance in this connection relates to the extension of mistletoe-infected areas. There exist quite obviously local centers of infection. These are most easily seen in cases where a large area is occupied by an open stand of mainly one species, such as the mesquite at San Antonio and the blackjack oak at Calvert. In traversing such timber lands one notes here an area of some square rods or acres in which almost every tree is infected, followed by a long stretch of timber land practically free from mistletoe.

METHODS OF COMBATING THE MISTLETOE.

An understanding of the habits of mistletoe, especially with respect to the mode of spreading the infection, will suggest that the surest way to prevent further spread of infection to new hosts would be to prevent any berries from ripening. This would imply, of course, the virtual extinction of mistletoe from any given community, and it may be questioned whether in spite of its harmfulness such an extreme measure is desired. As stated in the beginning, mistletoe has in many cases, if not generally, a traditional hold upon the regard of people which goes far toward condoning its harmfulness. It is reported that a certain prominent citizen in improving his residence property caused the branches to be pruned from one of his trees and mistletoe to be substituted therefor. (By what means and with what success is not stated.) Possibly one of the chief causes of the present conditions lies in the fact that in tolerating the growth because of its biological interest and because of its traditional setting the parasite has insidiously multiplied upon trees until it has become positively a pest. Those who have tried ineffectually for a decade or more to rid valuable shade trees of mistletoe will doubtless be ready to waive considerations of sentiment and tradition in favor of a radical movement looking to the extermination of the parasite.

The immediate problem is to deal with trees which are already infected. Here, again, a knowledge of the habits of mistletoe will show that where the infection is upon small branches careful pruning of these a few inches below the point where the parasite is attached to the branch will effectually get rid of it. The chief difficulty in this case is simply that of getting up high enough in the tree to do the pruning properly. This difficulty would be materially lessened by employing the common device in which pruning shears are attached to the end of a pole. The shears are operated by means of a heavy cord attached to the free lever arm. No indiscriminate lopping of branches or breaking them off with ragged fractures should be tolerated. Where, however, the infection is in the larger branches or on the trunk in which the cortical roots of mistletoe have ramified for years, and where innumerable sinkers penetrate the wood, the task of riddance is altogether more formidable. The embedded parts of the parasite are just as tenacious of life as are the rootstocks of Johnson grass, so that scraping or breaking off the external growth results, as in Johnson grass, in the sprouting up of more plants. Mistletoe, however, can be kept well under control by cutting off these successive crops of sprouts, and where this is done every year or two the trees are kept more sightly and the damaging effects of the mistletoe reduced to a negligible quantity. This method of treatment is the one most employed by those who devote any care to their trees; and it is here recommended as the most advisable procedure, except in cases where a skillful tree specialist is in charge.

The mistletoe plant is so brittle that it may easily be broken off, and by means of a hook attached to a long pole there is little difficulty in reaching any branches too large to be advisedly cut off. A better way, however, is to use a pruning hook attached to a pole. By this means the mistletoe may be cut off level with the bark and also many of the undeveloped buds destroyed, besides leaving the branch with a better appearance. The time and trouble, or the expense, required to keep trees free from mistletoe outgrowths in this way are really slight, compared with the advantage to be gained. A ladder of some kind, a pruning hook made by a blacksmith at the cost of perhaps a dollar, and two or three hours every year devoted to cleaning each tree will represent an average outlay. Naturally the best time to do this will be during the winter after the leaves have fallen, so that the mistletoe shoots may be more readily seen, but before the berries have become ripe enough to scatter the infection. If, however, the trees are gone over every year, or even every second year, there will probably be no question of berries on such young mistletoe shoots, and in that case the tree cleaning might better be done in the spring, when the parasite is ready to develop new shoots, thereby checking the new season's growth more effectually. This can be done before the new leaves on the host tree are large enough to conceal the mistletoe. In cases where the tree is full of mistletoe bunches the first cleaning up will naturally represent a greater outlay, for of course this will include the pruning of small infected branches, which is the most difficult and time-consuming item. In the larger towns and cities it is possible to employ experienced help in cleaning the trees of mistletoe, and this at no greater cost than that just indicated.

In some instances trees become so thoroughly infected that all the larger branches are sawed off close to the trunk, thus sacrificing the entire crown. In a dry climate like that of central Texas this is almost equivalent to sacrificing the tree permanently, for even though new branches are put forth the violent drying out at the sawed-off end of the branch extends back to the new branches, and they are killed. In such a case there would manifestly be much help in painting the cut surface with a heavy coat of tar or asphalt paint, or some other waterproof substance. This is advised in any case where a wound is made, as in scraping with a pruning hook or in cutting off small branches. It is questionable whether wholesale lopping-off of large branches is ever advisable.

POSSIBILITY OF ELIMINATING OLD INFECTIONS.

Can mistletoe be completely eliminated from large branches or trunks without fatal injury to the host? This bulletin does not pretend to give a satisfactory, or at least a final, answer based on sufficient demonstration, but it may present a statement of the case in the hope of calling forth more activity in the way of attempts to solve the problem practically.

Under the writer's direction, branches of a 10-inch hackberry were painted or smeared with the following preparations: (1) A strong wood preservative known as "carbolineum," (2) asphalt paint, and (3) laundry soap. In each case the mistletoe was shaved off flush with the bark before the preparation was applied. Also in each case a space was treated with the preparation and left without further covering, while a similarly treated space was wrapped closely with burlap. At the end of fourteen months (July 2, 1908) the report was as follows:

(1) Where carbolineum was used no mistletoe appeared, whether the branch was wrapped or not. The preparation had not perceptibly injured the branch.

(2) Where asphalt paint was used and the treated space not wrapped, mistletoe reappeared, but not until the following season. Where the treated space was wrapped, no mistletoe appeared after the wrapping was removed, eleven months from the date of its application.

(3) Where laundry soap was used mistletoe promptly reappeared as vigorously as before it was cut back and treated. On the wrapped branch mistletoe began to sprout up as soon as the wrapping was removed at the end of eleven months.

This report would seem to indicate that a strong preservative like wood creosote or carbolineum may be applied with a brush or cloth in quantity sufficient to kill mistletoe, without seriously injuring the branch or tree. Also that milder preparations, such as asphalt paint, coal tar, and white lead, may be applied with the result of checking the development of young mistletoe shoots, and by the additional precaution of wrapping the branch the parasite may be effectually killed.

TREE SURGERY AS APPLIED TO MISTLETOE INFECTION.

Another method of treatment will have suggested itself in the case of infected limbs which are too large to be advisedly cut off and in cases where the trunk is infected. Since the repeated development of mistletoe shoots takes place from buds formed on the cortical roots and since these roots extend only in the soft bark (cortex), why not cut away the bark and cortex down to the zone of young wood at these infected places? If the infection is a recent one or if the infected area is very small this would be a simple matter of applying a gouge or chisel locally, care being taken to cut far enough from the point of attachment of the mistletoe to include the spreading cortical roots. Thus there would result a small wound from 1 to 4 inches in diameter and extending into the branch perhaps one-eighth of an inch below the inner margin of the soft bark. This should be treated with an antiseptic wash, as indicated later, and painted with asphalt paint or coal tar or lead in oil.

In the case of old infection where the cortical roots have spread widely the removal of infected tissue could be accomplished also by means of chisel and mallet, but in such cases the size of the wound becomes a serious feature. In most cases of this sort it would be better to combine the surgical method with the chemical treatment and wrapping previously described. Thus with a chisel and mallet cut out each shoot or bud or bit of exposed cortical root of the mistletoe, making no wounds larger than the diameter of the shoot or bud removed; then paint with carbolineum and wrap with burlap, or treat with an antiseptic wash and then paint with asphalt paint, coal tar, or other waterproof dressing.

In this connection a word may be said about the general subject of mutilation of trees and the treatment of wounds in trees.[a] It should be understood that every wound on a tree invites disease from some fungous or bacterial infection. Unwise or careless pruning or trimming of trees is a source of much ultimate and really preventable damage. It is of course necessary to cause these wounds, but to leave them ragged and undressed is not necessary, nor is it any more rational than it would be to treat animals by the same cruel system of surgery. Whenever a wound is made on a tree, whether in ridding it of mistletoe or from whatever cause, it should be disinfected and dressed so that no disease spores can enter while the wound is healing over. The antiseptic wash may be prepared by dissolving 1 part of corrosive sublimate in 1,000 parts of water;

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[a] For further advice in this connection, see "Pruning," Farmers' Bulletin 181, by L. C. Corbett, and "Diseases of Ornamental Trees," by Haven Metcalf, in Yearbook, U. S. Dept. of Agriculture, for 1907.

or copper sulphate may be used, in which case 1 pound of the sulphate in 5 gallons of water makes a suitable wash. The protective dressing which follows this disinfectant usually consists of coal tar, but asphalt paint, white lead, grafting wax, etc., are used with good results. The edges of the wound should be left clean and smooth to facilitate the formation of wound tissue by which a tree attempts to heal over its wounds. In very dry seasons this dressing of tar or paint prevents the undue drying out which is apt to follow the cutting off of a branch. In unprotected stubs this drying out may kill the tissue several inches back of the cut end, and thus kill also the newly forming shoots, besides eventually causing a diseased spot. This precaution should especially be heeded by those who follow the practice—common in central Texas—of transplanting closely pruned trees, especially the young hackberry and cedar elm. The common custom of transplanting such trees without a ball of dirt around the roots and pruned back almost to the trunk is not advised as the best way to secure a rapidly growing, healthy shade tree; but if it is followed, surely the cut ends of the stubs should be painted to prevent drying out.

THE CARE OF TREES.

Perhaps after all is said it still remains that the most fundamental question involved in the enterprise of combating mistletoe is that of the selection and care of trees. It seems pretty obviously a case of neglect where a tree is allowed to become burdened with dozens of bunches of mistletoe until it becomes a deformed, unsightly object or completely destroyed. As a matter of fact, shade trees in well-kept grounds never do become so severely infected, or if they came into the careful owner's possession much infected their condition has been vastly improved. The trees which die of mistletoe infection are, in the majority of cases, those which stand along public highways, in unfenced or unimproved town lots, about neglected or abandoned residences, etc. They simply die of neglect.

That both the hackberry and cedar elm—the species which suffer most from mistletoe at Austin—may be kept healthy and free from mistletoe has been well demonstrated in numerous cases, but perhaps in none more strikingly than in that part of Austin which surrounds the university campus. This quarter has long been a center of harmful mistletoe infection. To the writer's personal knowledge numbers of trees have been killed outright by the pest in that vicinity. Plate I, figure 2, shows characteristically infected cedar elm trees standing opposite the west entrance to the campus. Just at the north of the campus are residence grounds bordered at front and side by a row of mixed cedar elm and hackberry trees. These trees are noteworthy for their vigorous and symmetrical growth and also for the fact that they have made an incomparably more rapid growth than certain specimens of the same kind of trees less favorably planted on the adjacent campus. Moreover, they are and have always been practically free from mistletoe. The pest has never gained a damaging hold upon these trees. Their freedom from it and their vigorous status otherwise are due to the exercise of a reasonable amount of intelligent caretaking which began with their being well planted in the first place.

It would be a misrepresentation of public sentiment to say that there is any lack of appreciation of trees or that careful attention is not given them; but it is fairly just to say that this appreciation and care are scarcely proportional to the large measure which trees contribute to human comfort and contentment and to the long time required to bring them to the stature where they do so contribute. Viewed from this aspect, all the minute details of care and treatment implied in the foregoing suggestions become fully justified. It would be rational, furthermore, to inquire whether, in view of the great value of the individual ornamental tree, it would not be worth while to abandon the custom of grubbing up the trees and setting them out like posts in favor of the more laborious and expensive but ultimately more profitable way of lifting each tree with its ball of earth and setting it in a well-prepared place with the least possible disturbance of its roots or mutilation of its crown. Even very small saplings thus carefully transplanted will eventually outstrip the very much larger transplanted "posts".

ORGANIZED EFFORT IN THE CARE OF TREES.

The specific problem of the eradication or control of mistletoe, as well as the broader one of selection and care of shade and ornamental trees, is of the kind to be taken up by some organization devoted to civic improvement. A well-organized, well-informed, and well-directed public sentiment would speedily solve these problems. The public schools may be made active allies of the movement in behalf of the care of trees, both in receiving and in disseminating information, and in otherwise arousing an enthusiastic spirit. City and county officials may by special enactment be authorized to include in their supervision the care of trees in public parks and along streets and highways. The individual owner may be led to feel a larger responsibility for the welfare of his trees, both for the benefit they bring him and for the relation they sustain to the welfare of the community at large.

THE COMMERCIAL IMPORTANCE OF MISTLETOE.

Mistletoe is used in Christmas decorations more or less throughout this country, but especially in northern cities. Within the range of the plant it is employed more or less in this way, especially by those to whom it is still a novelty. Countless packages of it are sent through the mails and by express to friends in the North. There is, however, a well-defined Christmas trade in mistletoe by which the markets in the North are supplied. The choicer and more expensive grades are handled by southern florist supply firms. Only well-berried shrubs are used in this trade, and these are crated with great care to insure against shattering and freezing in transit. These shipments reach the retail trade through the agency of northern firms dealing in florists' supplies. Even larger quantities of mistletoe are retailed in the northern markets by grocers and market men. These supplies are handled with less care and are cheaper than florist-trade mistletoe. Some of these supplies come from southern dealers in general merchandise, who add the handling of mistletoe as a special holiday feature of their business. The mistletoe is brought in by countrymen and its value taken in trade. It is then packed in barrels or crates and shipped to northern commission houses, and by them distributed to the retail grocery and market trade.

Apparently this Christmas trade has drawn upon mistletoe supplies only in relatively few localities. So far as the general supply is concerned the market might be widely extended. Judging by the appeal which this curious plant makes to the average person it would appear to be possible to greatly multiply the purchases of it throughout the North in smaller cities and towns, as well as in the larger, to which the market seems at present to be largely limited. On the other hand, there is constant inquiry from districts in which mistletoe is abundant for information as to the possibility of finding a market for it. An increased demand for mistletoe for Christmas purposes would constitute an important factor in the control of mistletoe as a pest, but as a matter of fact it is unlikely that the plant will ever be regarded very generally in that light.

SUMMARY.

(1) In general, the American mistletoe, like its European prototype, is more cherished because of its biologic interest and historic setting than feared for its harmfulness to trees. In some districts, however, notably in central Texas, its destructiveness as a tree parasite outweighs other considerations in its behalf.

(2) The region in which mistletoe is most destructive coincides with the transition from a humid climate favorable for forest growth to a dry climate less favorable for trees, and where the effects upon tree growth are such as to furnish the parasite more favorable light

conditions than in the closer stands and denser foliage of humid climate forests.

(3) The harmfulness of mistletoe is due in part to its mechanical injury to trees (deformity of branches and trunk, wounds followed by decay), but more especially to its drain upon the trees' vitality by withdrawing water and nutriment substances from them. The sinkers which connect the parasite with the water-transporting vessels of the wood and the cortical roots which ramify in the soft bark are the means by which the parasite withdraws substances from its host.

(4) The first infection of a tree by mistletoe takes place only through the agency of a germinating seed placed upon the body or branch of the tree by birds (mostly mocking birds, wax wings or cedar birds, and robins), except in the rare case where berries fall upon a branch from a bunch of mistletoe in an overtopping adjacent tree. The subsequent spread of infection upon a tree may take place by the falling or washing of berries upon other parts of the tree from the previously established mistletoe shrubs, or by the spread of cortical roots from which new mistletoe shoots arise. Spreading by cortical roots occurs more readily upon some species of trees than upon others, and is especially stimulated by the injury or removal of the original shoot.

(5) The mistletoe seed and seedling exhibit unusual powers of resistance to drying out, and are thereby enabled to survive in considerable numbers the critical period from the time the berry is placed upon a branch until the parasitic plantlet becomes established. This period may extend beyond the first growing season.

(6) A tree may become infected at any point where living tissue is exposed or covered only by a thin layer of cork with breathing pores, but the most vulnerable points are the young branches and, sometimes, buds. The sinker of the mistletoe seedling is able to penetrate certain tissues by dissolving the walls of cells lying in its path. It is uncertain whether cutinized or corky cell walls can be so dissolved, but the writer believes that they can.

(7) The trees most liable to infection are those which occur singly or in clumps or rows along streets and highways, in vacant lots and parks, along the border of fields, and narrow strips of timber along streams. The damage to trees in forest stands is negligible. Shade and ornamental trees suffer most.

(8) While it is not certain that any broad-leaved tree is wholly immune to attack from the American mistletoe, some are practically so, although freedom from infection seems to vary with locality. In the choice of trees for planting the question of the ability of a tree to resist infection might profitably be considered. It is believed that any tree subject to infection may be infected by seed from mistletoe growing upon any other species; e. g., the hackberry may be infected

by seeds of mistletoe grown on the elm, the live oak from those on the mesquite, etc.

(9) The damage to trees may be very largely overcome by breaking and scraping off the bunches and scattered sprouts of mistletoe every year or two. If the parasite is attached to small branches these may be pruned off a few inches below the mistletoe, and thus the infection be wholly removed at that point.

(10) Infection upon old branches and upon the trunk is very difficult to get rid of, because the cortical roots spread freely in the soft bark and any piece left there may give rise to new mistletoe sprouts. Since the cortical roots do not extend into the wood (of course sinkers do), the removal of the hard and soft bark clean to the wood about an infected spot should exterminate the parasite at that point. The objection to this method is that it necessitates large wounded surfaces. Such wounds should always be disinfected and afterwards coated with tar.

(11) In some cases mistletoe has been killed from old branches by the application of chemicals, which is made more effective by subsequently wrapping the limb with burlap. Thus carbolineum alone, and asphalt paint with burlap wrapping, were found to eliminate the infection.

(12) It is suggested that a combination of the above methods would be effective. First, remove with gouge or chisel the exposed shoots or buds of mistletoe down to the wood without making large wounds; fill the larger wound holes with tar, and paint the whole surface with carbolineum or with asphalt paint. When asphalt paint is used wrap afterwards with burlap.

(13) The cutting off of large branches in order to get rid of mistletoe is to be discouraged. It is apt to injure a tree more than the mistletoe would, particularly if the latter be broken or scraped off every few years.

(14) Every wound on a tree, e. g., those caused by digging out mistletoe or by cutting off branches, is a point of attack for disease-causing germs. Such wounds should always be disinfected and painted with tar or some similar waterproof coating.

(15) The mistletoe question resolves itself largely into the question of the care of trees. The spoiling or killing of trees by mistletoe is due chiefly to neglect. A well-organized movement in behalf of civic improvement would help to remedy this defect. City and county officials who have charge of streets and parks and public highways should be required to see that trees on public ground are kept free from mistletoe.

(16) The use of the mistletoe in Christmas decorations gives it a commercial status which has some bearing on the question of its control and extermination.

DESCRIPTION OF PLATES.

Plate I. Fig. 1.—An isolated hackberry tree near Belton, Tex., with innumerable bunches of mistletoe. This tree is in its winter condition, being absolutely without leaves of its own. Fig. 2.—A cedar elm tree on a vacant lot in Austin, Tex., showing its winter condition. All the foliage is mistletoe.

Plate II. Fig. 1.—A water oak tree in a creek-bottom field near Bryan, Tex. Numerous bunches of mistletoe 2 or 3 feet in diameter are shown at the ends of the slender branches. Fig. 2.—A deformed branch of a hackberry tree which has been infected by mistletoe for ten or twelve years. The dwarfing of the branch beyond the place of infection is shown. The original mistletoe plant has been destroyed, leaving a decayed spot. Young shoots of mistletoe from adventitious buds.

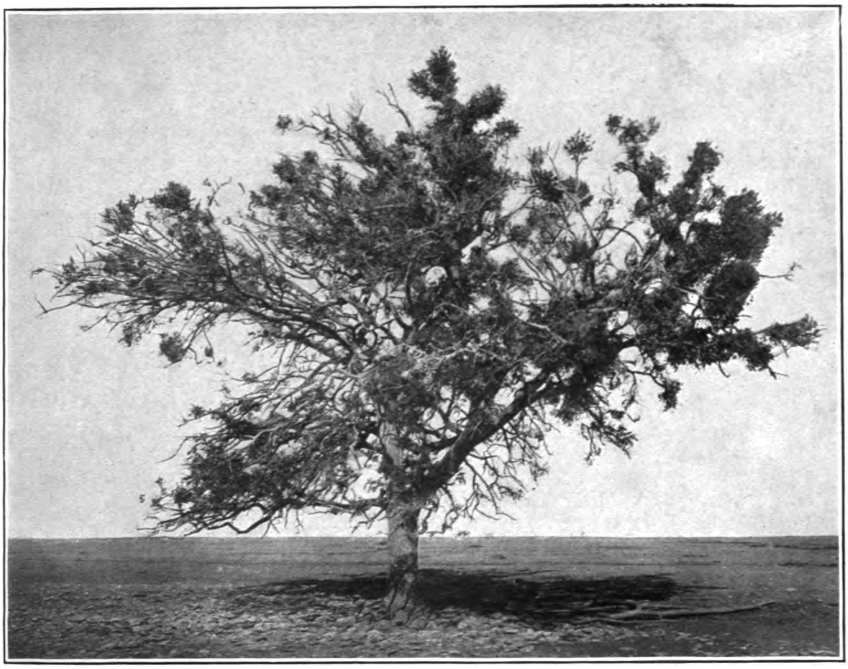

FIG. 1.—AN ISOLATED HACKBERRY TREE NEAR BELTON, TEX., WITH INNUMERABLE BUNCHES OF MISTLETOE.

This tree is in its winter condition, being absolutely without leaves of its own.

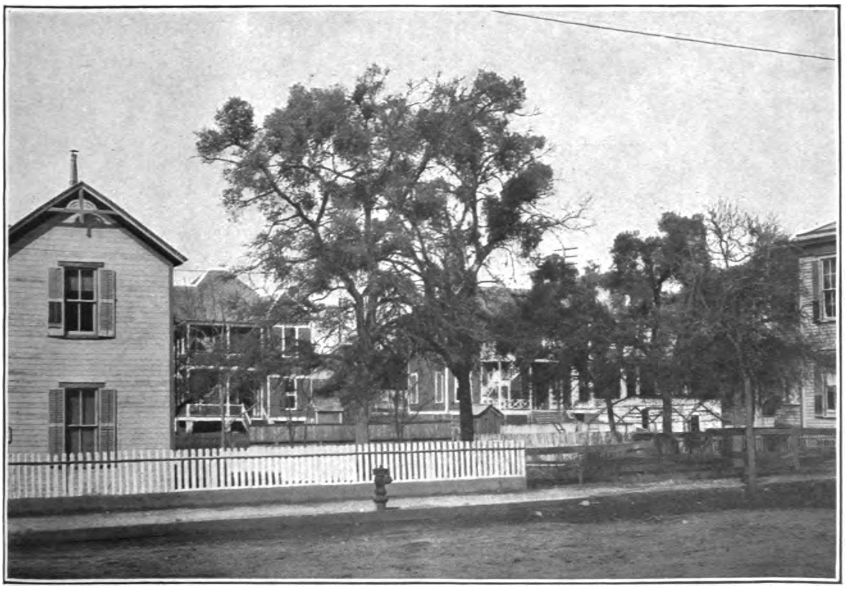

FIG. 2.—A CEDAR ELM TREE ON A VACANT LOT IN AUSTIN, TEX., SHOWING ITS WINTER CONDITION.

All the foliage is mistletoe.

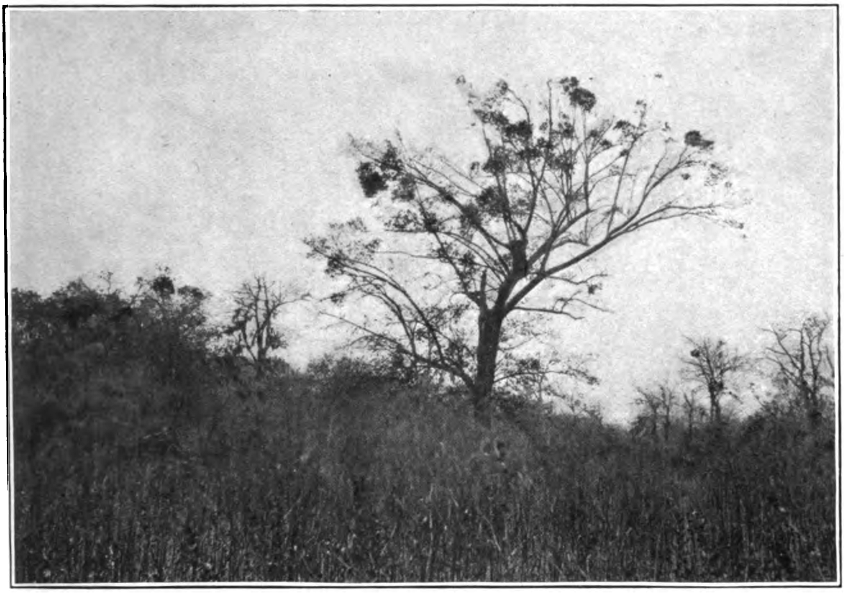

FIG. 1.—A WATER OAK TREE IN A CREEK-BOTTOM FIELD NEAR BRYAN, TEX.

Numerous bunches of mistletoe, 2 to 3 feet in diameter, are shown at the ends of the slender branches.

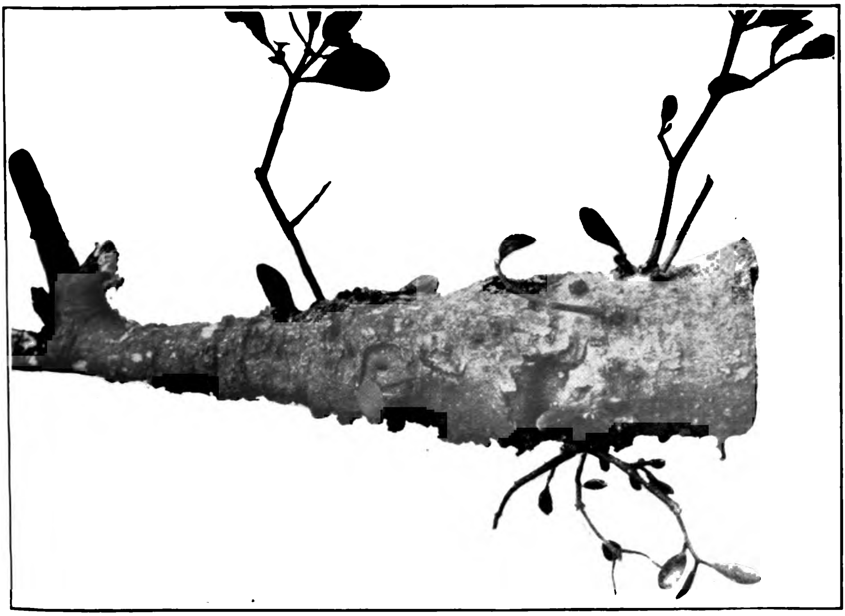

FIG. 2.—A DEFORMED BRANCH OF A HACKBERRY TREE WHICH HAS BEEN INFECTED BY MISTLETOE FOR TEN TO TWELVE YEARS.

The dwarfing of the branch beyond the place of infection is shown. The original mistletoe plant has been destroyed, leaving a decayed spot. The young shoots of mistletoe seen are from adventitious buds.

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B. T. GALLOWAY, *Chief of Bureau.*

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FOREIGN SEED AND PLANT INTRODUCTION.

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LETTER OF TRANSMITTAL.

U. S. Department of Agriculture,
Bureau of Plant Industry,
Office of the Chief,
Washington, D. C., September 25, 1909.

Sir: I have the honor to transmit herewith a manuscript entitled "New Methods of Plant Breeding," by Mr. George W. Oliver, Plant Propagator of this Bureau, and recommend that it be published as Bulletin No. 167 of the Bureau series.

Respectfully,

B. T. Galloway,
Chief of Bureau.

Hon. James Wilson,
Secretary of Agriculture.

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NEW METHODS OF PLANT BREEDING.

INTRODUCTION.

A few years ago Dr. B. T. Galloway, Chief of the Bureau of Plant Industry, mapped out some plant-breeding work for the writer which involved crossing varieties of lettuce, alfalfa, and cowpea, and also certain species of Poa, Trifolium, Melilotus, etc. The work in the beginning presented many difficulties which have since been overcome, and it is now progressing satisfactorily.

The improvement of plants by cross-breeding varieties is gradually becoming an important factor in the culture of many of our field and garden crops. The majority of intentional crosses and hybrids made in the past represent work which has been easy of accomplishment. The more difficult subjects have been passed by or at most the efforts of breeders with the hitherto refractory genera have to a large extent been nullified by natural obstacles in the path of success.

The only difficult part of plant breeding lies in knowing just how to make the most of a cross or hybrid which has been secured. The literature on this subject which has appeared during the last few years is apt, unfortunately, to lead the beginner and even the practical breeder into a maze, and he may conclude that the subject is too complex for comprehension.

This should not cause discouragement, however, because the mission of the plant breeder is to produce varieties which are in some measure improvements over the old ones, and each advance made will tend toward that perfecting of plant life which will insure better products for man and the domestic animals.

The present contribution to the subject deals not with laws, but with methods used by the writer in accomplishing what have hitherto been considered impossible or difficult crosses, and they may prove helpful to others engaged in the same line of work.

Until recently it has been found impossible to cross many plants owing to the fragile nature of the sexual organs. This difficulty has been removed, and the process whereby it has been accomplished is here described for the first time.

There are numerous plants, also, both ornamental and economic, the flowers of which are so small that their stamens are very difficult to remove in the process of emasculation, and this fact has undoubtedly contributed largely toward delaying the rapid improvement of many flowering plants, fruits, and vegetables by cross-breeding and hybridizing. Mendel, who did so much in his particular line, worked with two genera only: Pisum and Hieracium. The former is easy to manipulate, but all the species of Hieracium present difficulties in emasculation which by the ordinary methods are practically insurmountable. In fact, Mendel found them so great that he did not finish his work on this genus. Nevertheless, in the flowers of the hieraciums, and many other plants regarded as equally difficult, the pollen can be thoroughly removed, and with as great facility as in those of the rose or any other flower in which the reproductive organs are large and easily handled. This new process, which may be called "depollination," is the removal of pollen from the stigma before fecundation has taken place. It is applicable to flowers in which emasculation is impracticable because of the minuteness or delicacy of the floral organs. It is hoped that this newly found method of preventing fecundation by undesirable pollen will be instrumental in furthering the projects mapped out by the ever-increasing number of plant breeders.

The writer has worked on several genera of the Compositæ with complete success. The method here described can be used not only with the Compositæ, but also with all flowers having reproductive organs too small to be successfully manipulated by the ordinary methods of emasculation. The use of the method does not stop here. It can also be applied to the stigmas of larger flowers when there is any doubt whether pollen has recently gained access to the stigmas previous to artificial pollination.

ORIGIN OF THE NEW METHODS OF PLANT BREEDING.

During the spring of 1903 work was begun on the crossing of certain varieties of forcing lettuce. When the plants came into flower it was at once apparent that the problem of emasculation was a knotty one. The flower heads are small and the florets themselves will scarcely bear handling because of their very fragile nature. In one or two instances the stamens were removed, but always with sufficient injury to the remaining parts of the flower to cause it to wither. A flower of lettuce is in fact about as difficult to manipulate by the usual methods of emasculation as it is possible to conceive.

When the flower head expands, the anthers have already dehisced, and the unexpanded stigmas are covered with pollen. (See Pl. I, fig. 1.) The stigmas begin to expand at the tips, and simultaneously masses of pollen fall on the inner surfaces, to which the pollen closely adheres.

In the bud stage the parts of the floret are so easily damaged that endeavors along this line of attack were quickly abandoned. Having read somewhere that pollen grains would adhere readily to the end of a piece of sealing wax previously rubbed briskly, wax was tried, but without success. The idea then suggested itself that the pollen might be successfully removed with a dampened camel's-hair brush. This plan was also a failure, because with the operation ever so carefully performed some of the pollen grains were left on the stigmas.

Success finally came, not with the aid of a camel's-hair brush or sealing wax, but with the aid of the garden hose. A robust plant of the Grand Rapids variety of lettuce opened 15 flowers one morning, and within as many minutes every flower was successfully depollinated. The metal attachment on the end of the hose was cut off; a piece of hose of smaller diameter was placed in the end of the other hose; then a piece of soft rubber tubing of small diameter was placed inside the second piece of hose and the water turned on just enough to do a little more than trickle. By squeezing the end of the rubber tubing (see Pl. I, fig. 2) a very tiny jet of water was secured. This was trained on the lettuce flowers, and perfect depollination resulted.

After the tiny jets of water had played on each flower head for a few seconds not a trace of pollen was to be found and the pistils stood out from the ligules strong and unharmed. Small pieces of blotting paper freely applied to the florets edgewise soon absorbed all of the water. Pollen from the flower of another variety was then applied. In each of the 15 heads of flowers, seeds matured, and all of the resulting seedlings proved to be intermediate between the two parents.

In depollinating, the flower head is held securely between the thumb and the first and second fingers, and in pollinating it is similarly held. In applying the pollen to the stigmas one head of flowers from the pollen bearer is used, or more than one if sufficient pollen is not deposited on the stigmas. Before applying the pollen a few or all of the ligules should be cut off from the pollen-bearing head of flowers, leaving only the pollen-covered stigmas, and the remaining part of the head applied to the flowers which have been depollinated, working it among the stigmas with a circular motion.

In pollinating lettuce flowers and those of other genera in this division of the Compositæ there is not the same necessity for depositing the pollen on the stigma of each floret as there is on the flowers of the plants of the other divisions, because the lettuce flower heads close very soon after pollination. This act of closing will almost certainly cause the slender stigmas to become well covered with pollen because, in the act of pollinating, the ligules are apt to harbor many grains of pollen.

The first cross effected was between the varieties of lettuce known as Grand Rapids and Golden Queen, the former being the seed bearer. A short account of the subsequent behavior of the seedlings may be of interest here as a guide to similar experiments in the future.

The crossing was commenced about the beginning of July. From the application of pollen to the ripening of the seed, sixteen days elapsed, the time varying slightly according to the condition of the weather—warm, dry weather accelerating the ripening period.

The seeds were sown in the latter part of December in order to make certain that the seedlings during the later stages of growth would have the benefit of warm weather and thus insure seed production.

Seeds of each parent were also sown separately for comparison with the crosses in all stages of their growth. Even in the cotyledon stage differences were noted between the cotyledons of the crossed seeds and those of the parents; they were uniformly not as light in color as those of the Grand Rapids, neither were they as deep a yellow as those of the Golden Queen, but any doubt arising as to the differences in color, size, and form of the cotyledons of the crosses compared with those of the parents was dispelled as soon as the first character leaves appeared in the crosses. The first leaf of the cross Grand Rapids × Golden Queen was similar in every respect to the first leaf of the cross Golden Queen × Grand Rapids, thus proving beyond a doubt at that early stage that the mere act of crossing had been a success. The plants of the two crosses could not have been distinguished, so similar were they in appearance.

A large-sized Grand Rapids lettuce, but more yellowish in appearance than that variety, with the leaves slightly less crumpled and the margin less fringed, would be a fairly accurate description applicable to both lots of plants of the first-generation crosses.

Seeds harvested from each of the plants were labeled and sown separately. In the second generation the results were rather bewildering. The seeds from each plant of the first generation gave approximately 30 distinct forms, and out of the entire number of seedlings of the different numbers about 60 distinct forms were noted. Forty-five plants of these were selected for further testing, and it so happened that the plant numbered 39, selected as being the best in the field, gave the most promising progeny when sown indoors. Several were then selected for fixing. Four distinct forms have come true from seed in 1908. The fifth and last of the heading varieties up to that time had about 15 per cent of seedlings resembling the Grand Rapids variety. By selecting seed from each of 36 of the best heading individuals and sowing separately, about two-thirds of the lots have come true. These will be tested still further before being sent out for trial.

TOOLS REQUIRED FOR DEPOLLINATION AND EMASCULATION.

A small pair of scissors is necessary to remove parts of corollas, stamens, etc., of the different flowers. Those shown in figure 1, *A*, are more convenient for use on many subjects than the common scissors, as they can very readily be adjusted to the various needs with one hand. A medium-sized pair of the ordinary kind of scissors used by plant breeders, with blades 1 inch in length, figure 1, *D*, is also necessary.

Forceps are indispensable tools. Those forceps in common use would be better adapted to the needs of the plant breeder were they supplied with a flattened pin attached to the handle (see fig. 1, *C*). This would often prevent the necessity of laying down one tool to take up another while the operator is performing a delicate piece of work and while the eyes are perhaps fixed on a very small object. A needle can be tied on very easily and the combination is an exceedingly useful one. Several pairs of forceps which are self-closing (shown in fig. 1, *B*) are necessary in such lines of work as pollinating depollinated stigmas of alfalfas and many other small flowers. These forceps enable the operator to hold a stamen or a sexual column of a small legume while pollinating. It is difficult to perform this work satisfactorily with the fingers.

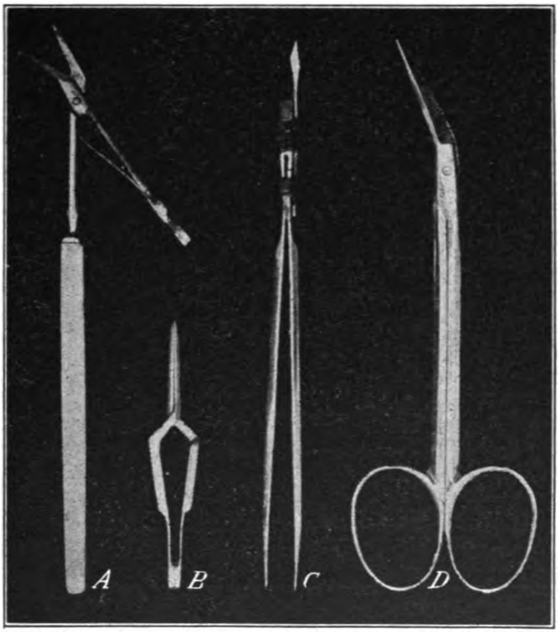

FIG. 1.—Tools used in depollination and emasculation: *A*, scissors useful in removing small organs; *B*, self-closing forceps; *C*, forceps with attachment; *D*, scissors for severing large organs.

Watch glasses and small-sized moist chambers are needed to preserve pollen. Tags for keeping records while the seeds are ripening, ranging from one-half inch by three-quarters inch to those of much larger dimensions, are indispensable. Some small-sized camel's-hair brushes, some good white blotting paper torn into small pieces, and a lens should also be included in the kit.

DEVICES USED IN DEPOLLINATING FLOWERS.

The contrivances required for the work of depollination by water are inexpensive and easily secured. When the method was first used attachments to the garden hose were employed, but these were found too clumsy and uncertain; moreover, the hose is not always available when it is desired to depollinate flowers in the field. A fairly good substitute is a modification of the common putty bulb (fig. 2, *E*). This answers the purpose very satisfactorily for large flowers of the Compositæ, Leguminosæ, and other groups. The putty bulb will hold about a pint of water. By unscrewing the spout or ejector, the rubber bag may be quickly filled with water and the ejector replaced in a few seconds. The size of the jet of water is regulated by using a suitable piece of bamboo reed or other contrivance fixed firmly in the tube. When the bulb is full of water a slight pressure with the hand will cause a fairly strong but fine stream of water to be emitted.

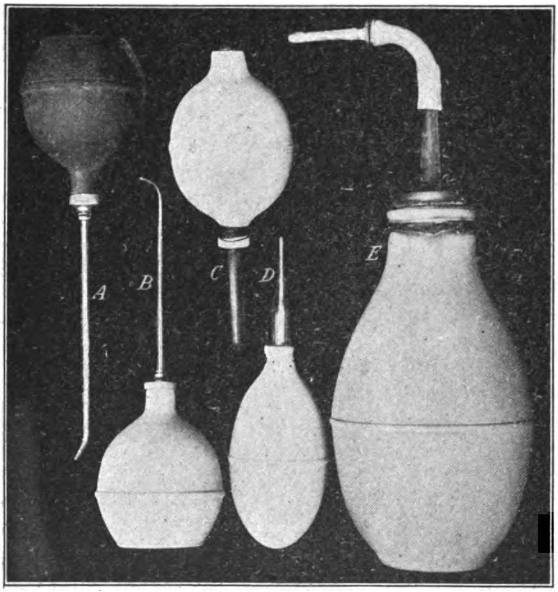

FIG. 2.—Devices used in the depollination of flowers: *A* and *B*, chip blowers or water bulbs; *C*, water bulb with valve at bottom provided with celluloid ejector; *D*, old rubber bulb with glass tube inserted; *E*, "putty bulb" with attachment to give a small jet of water.

It will be found that a very small jet of water is needed for very small and fragile flowers. For this purpose the various kinds of chip blowers (fig. 2, *A* and *B*) and water bulbs sold by dental supply companies suit the plant breeder's needs admirably. These devices are inexpensive, and when many flowers are to be treated at one time several of the chip blowers or water bulbs may be brought into use. As soon as the contents of one are exhausted and while the bulb is still pressed in the hand it may be put in a vessel of water; then when the others are emptied of their contents the first one will be ready to be used again.

There is a still further choice in instruments of this nature in the shape of rubber bulbs (fig. 2, *C* and *D*) similar to those used on cameras.

A piece of glass tubing can be pushed into one of these; the other end of the tube can be brought to a fine point by heating it in a flame and breaking off the point, leaving an aperture about one-sixteenth inch in diameter. This device does satisfactory work, but the others are preferable.

EMASCULATION.

A necessary preliminary to successful plant breeding by hybridization or cross-fertilization consists in preventing pollen of the plant used as the seed bearer, or pollen from other plants of the same variety or species, or pollen of any other closely allied variety or species from gaining access to the stigmatic surface of the flower intended to be pollinated instead of the pollen selected by the operator.

With the greater number of plants, especially those having stamens of large size, emasculation is a simple matter, and consists of removing the stamens before the anthers shed their pollen. Examples of plants having large stamens are found in the rose (see Pl. XI, fig. 1), cherry, peach, etc. The poppy, carnation, and tobacco are also familiar examples in which emasculation is an exceedingly easy process, as the stamens can be removed before dehiscing with a pair of forceps.

OBSTACLES IN EMASCULATING THE FLOWERS OF COMPOSITÆ.

It is well known that the florets of the various genera of the composite flowers are so constructed that the anthers can not be removed without the florets being injured beyond recovery.

The anthers in the disk florets unite and form a tube (Pl. VIII, fig. 1, *B*, and Pl. IX, fig. 1, *B*) over and around the upper part of the immature pistil so that in the effort to remove this tube before the floret opens or the anthers dehisce the anthers are certain to be ruptured and the pollen scattered over the stigma. The parts of the florets are so small that it is practically impossible to remove the anthers in a young stage without ruining the florets. There is also great danger of injuring the very slender pistils during the attempted emasculation. Some genera have only female organs in the ray florets and both male and female in the disk florets, and in some important genera some species have sterile ray florets and depend on the disk florets alone for fertilization. (Pl. V, figs. 1 and 2.) But to depend on the ray florets alone for careful crossing means in all instances slipshod work, as the disk florets must then all be removed, causing too much mutilation of the flower head. Depollination of the disk florets by the method herein described (Pl. VIII, fig. 2, *B*) means that the work is absolutely certain to produce the desired results. Moreover, depollination of the disk florets followed by crossing is many times easier than the use of the ray florets as seed bearers, as this is necessarily followed by the removal of the disk florets to prevent self-pollination.

In several genera of the Compositæ it will be found that the staminal tubes are not drawn down into the tubular corolla until the second day after shedding the pollen. This happens with some of the species of Helianthus (Pl. IX, fig. 1, *B*), Gaillardia, etc. A short, sharp needle fixed in the end of a piece of wood less than the diameter of a pencil and 4 inches in length can be very successfully used in opening the collar formed by the united anthers around the stigma, so that it may be depollinated before the pollen grains germinate. All of the crop of florets which come out in any single day can be opened after the manner described, the pollen washed from them, and the flower head bagged, pollination being delayed until the following day, when the circles of florets contiguous to those already depollinated will have come to maturity. These are in turn treated with the needle and depollinated by water. The remaining unopened florets may then be pulled out with a pair of forceps, the two lots of treated stigmas pollinated at the same time, and the flower head bagged. A method still easier is to depollinate the two outer circles of stigmas and then remove them with the aid of a pair of forceps, which in the larger number of genera is easy of accomplishment. When the remainder of the florets expand, depollination is effected and the flowers are pollinated as soon as the flower head is cleared of water (Pl. VII, figs. 1 and 2). In all composite flowers which attract insects the head should be bagged to prevent undesirable pollen from gaining access to the stigmas after being pollinated.

It may be said that unless the method of depollination herein described is used with flowers of the Compositæ, especially those of the division Ligulifloræ, there is very little chance, if any, of absolutely certain results from cross-fertilization between different varieties of the same species or from hybridizing distinct species.

HOW HYBRIDS AND CROSSES OF COMPOSITE FLOWERS MAY HAVE ORIGINATED IN THE PAST.

It is quite possible that a long continuous shower will wash the pollen from the stigmas of a composite flower and that as soon as the sun shines these flowers are visited by insects whose bodies are occasionally covered with pollen obtained from florets of other varieties or species which open and shed their pollen, either before or subsequent to the pollen-removing shower of rain. It is certain that cross-fertilization may take place in this way. Those species and their varieties having infertile ray florets can be crossed only when the disk florets, containing both male and female organs, are used as the seed bearers. (Pl. VII, figs. 1 and 2.) All of the work in breeding composite flowers is rendered simple by the depollinating method. Especially is this the case with chrysanthemums, asters, dahlias (Pl. VI, fig. 2), marigolds, cineraria (Pl. VI, fig. 1), cosmos, zinnias, lettuce, and with all the numerous genera having infertile ray florets.

PREPARATION OF SEED AND POLLEN BEARING PARENTS.

Too much care can not be bestowed on isolating from insects the plants from which pollen is to be selected for use in crossing. This is a part of the plant breeder's work which is apt to be neglected. Pollen is usually considered satisfactory irrespective of the conditions under which the flowers have been produced. It is not unnaturally supposed that the pollen is pure while the flowers are in the bud stage, and although this is the case in many instances, especially where large numbers of one variety or species are growing side by side, yet there is no doubt that the pollen of these plants is often interchanged, as in alfalfa and other plants of the legume family in which the anthers dehisce in the flower bud and which are visited by the pollen-eating thrips.

Much experimental work in plant breeding by crossing and hybridization gives negative results through lack of care in the selection of pure pollen. It is just as necessary to protect the flower selected to supply the pollen, in order to prevent foreign pollen from being deposited on or near the anthers either by insects or by wind, as it is to protect the seed-bearing flowers. In selecting pure pollen it is a good plan to have isolated plants growing in pots in the greenhouse, where they can be protected from insects during the flowering period by wire screens. If this is not feasible, the flowers should be bagged when the buds are nearing the opening stage, to prevent insects from depositing pollen on or near the flowers. Absolute success means careful attention to the very minutest detail. Omission of the necessary care in this respect has undoubtedly caused a vast amount of work to be unproductive of good results. Not only should the pollen bearer be grown under glass, but in every case where it is possible the seed-bearing parent should also be grown in this manner in order to have the work absolutely under control. Even then with the aid of wire screens only the large insects can be kept from the flowers as the pollen-eating thrips found in nearly all flowers is one of the greatest carriers of pollen from flower to flower. It is not unusual to find one of these minute insects with several grains of pollen attached to its body, rendering the work of evidently careful emasculation of no avail. The plants infested with these insects should be treated to a slight fumigation with hydrocyanic-acid gas and afterwards protected with structures covered with some kind of fine white fabric to prevent the flowers being visited immediately before emasculation and until fertilization takes place.

CONDITION OF THE STIGMA AT THE TIME OF POLLINATION.

It has often been stated that the stigmatic surface of the pistil must be free from moisture when the pollen is applied. When the contrary condition is present, the pollen is said to be less effective than it would be were it applied to the stigma when free from moisture deposited from the atmosphere. Be this as it may, it is absolutely certain that pollen is as effective when applied to stigmas which have been thoroughly treated with water and the moisture adhering to them partly removed with the aid of bibulous paper applied edgewise as it is when the stigma has not come in contact with water.

THE APPLICATION OF WATER TO ALL FLOWERS.

For the removal of pollen which may have been deposited upon the stigma of a flower previous to pollinating, water should be used in every case where the flower has been exposed through inadvertence or otherwise to the visits of insects. Its use in such a case, if it be applied within a certain period after the pollen is deposited, is desirable, as it will render the operation of crossing with another flower more certain, because if pollen is present on the stigma of a flower, especially if the pollen be of the same variety or species as the flower which it is desired to use as the seed bearer, its own pollen will in many cases take effect in preference to the pollen of the flower of a separate species or variety.

Another case may be mentioned in which this adjunct to perfect emasculation can be used advantageously. It sometimes happens that an operator comes across an open flower of some kind which he may wish to cross, with the stamens already dehisced and the stigmas well covered with pollen. If the pollen has been deposited on the stigmas for only a short time, in most flowers every grain can be removed effectively by the aid of the depollinating method herein described. In the case of lettuce the flowers have been depollinated after the pollen had been in contact with the stigma for an hour and a half and a successful cross has followed.

CROSSING ALFALFA.

WORK ACCOMPLISHED IN THE PAST.

For the purpose of demonstrating how the new method of preparing flowers for crossing can be applied to a wide range of subjects, alfalfa may be taken as an example. While it is true that alfalfa crosses and hybrids are effected by insects, the genus is an exceedingly difficult one to deal with by ordinary methods of emasculation, and there is probably no record of intentional crosses among the many forms of *Medicago sativa*[a] or hybrids between it and other species, if we except those of Urban,[b] who succeeded in making reciprocal crosses with *Medicago sativa* and *M. falcata* in 1877. The work of Urban, however, was evidently done without taking the necessary precautions to preclude the possibility of error, as the pollination was a crude imitation of that effected by insects.

We can not afford to relegate the crossing of the varieties of this increasingly important plant to insects or to risk pollen of unknown or undesirable forms on the plants we wish to cross. If we were to copy the insect method, we should, of course, get crosses, but we should remain as much in the dark concerning the parentage of the seedlings as we have been in the past.

PECULIAR FEATURES OF THE WORK.

None of the species and varieties of alfalfa sets seed from self-pollination if the flowers remain untripped (Pl. II, fig. 1, *A*). The pollen in the untripped flower, being of a slightly adhesive nature, does not get an opportunity to move after being discharged from the anthers while still within the closed keel, and after the dehiscing period the surface of the stigma is protected from it by being close against the keel. This is the case with the flowers of most of the varieties, but there are forms the flowers of which often have the stigmas completely hidden by the pollen (see Pl. III, *C*), and yet even these do not set seed if the flowers remain untripped.

When, however, the flower is tripped (Pl. II, fig. 1, *B*), either by drawing the closed hand along the raceme or by snipping the individual flowers with the forceps, this action releases the column from its imprisonment within the keel and permits it to spring upward with a very rapid movement. In doing so the pollen grains are thrown on the banner in large numbers and the stigma falls with force among them, causing a mass of the grains to be embedded in it (Pl. II, fig. 1, *B*). This action usually results in fertilization.

When the flowers are visited by certain insects, the upper part of the sexual column falls with considerable force on the under part of the insect. The stigma in this case is then partly pollinated with pollen from the same flower, from other flowers on the same plant, or from flowers of other plants of the same variety or from other varieties, or from pollen of other species previously deposited on the body of the insect.

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[a] The botanical history and nomenclature of this species have been discussed in previous publications of the Bureau of Plant Industry; by C. S. Scofield in Bulletin 131, part 2, "The Botanical History and Classification of Alfalfa," and by Charles J. Brand in Bulletin 118, "Peruvian Alfalfa: A New Long-Season Variety for the Southwest."

[b] Urban, I. Verhandlungen des Botanischen Vereins der Provinz Brandenburg, vol. 19, p. 125. 1877.

OLD METHODS OF CROSSING ALFALFA.

Perhaps the method first used in crossing alfalfa, at least so far as can be ascertained, consisted in introducing a sharpened piece of wood, resembling in shape the proboscis of a bumblebee, into the suture formed by the blades of the keel of the pollen bearer. The piece of wood was dusted over with pollen secured by allowing a sexual column to trip on it. It was pushed into the suture of the flower of the proposed seed bearer, and the resulting tripping of the column caused the stigma to come in contact with the pollen already secured on the piece of wood, the supposition being that, in some cases at least, foreign pollen is prepotent over that of the seed bearer on its own flowers.

The second method—one which the writer tried several years ago—consists in emasculating the flowers in the bud stage, but as the anthers dehisce before the buds expand the operation must be performed when the buds are quite small, and the danger of bruising the flower enough to cause it to wither is great. This operation is easily performed with the aid of a binocular dissecting microscope, but even when the parts of the flower are left uninjured the method is clumsy and exceedingly uncertain.

Another method which involves a considerable element of uncertainty consists in planting one or more plants of a known variety in the midst of a large field of another variety. These plants are used as seed bearers and the work of pollination is left to the insects.

Thus it will be seen that when a cross of known ancestry is desired between two varieties of alfalfa the chances of securing it by methods heretofore in vogue are very remote.

NEW METHODS DEVISED BY THE WRITER.

A few years ago, while investigating methods of crossing alfalfa and trying to cross a hardy form of Peruvian alfalfa with a variety from Turkestan, it was found that there are at least three variations in the method of compelling this plant to capitulate readily to the wishes of the plant breeder.

DEPOLLINATION BY WATER.

The first method to be described requires close attention to details. The tools and other necessary material are as follows: Four pairs of forceps, three of them self-closing; a pair of scissors (see fig. 1, *A*); a few pins; a small chip blower such as dentists use (see fig. 2, *A* and *B*); a vessel of water; and some pieces of good blotting paper.

The operations of depollinating and applying pollen to the stigma can be performed satisfactorily with the unaided eye, but the operator should take his first lesson with the aid of a low-power binocular dissecting microscope. The magnification should not be higher than 8 diameters.

Three or four flowers on a raceme should be selected for crossing. The others may be cut off, although this is not necessary if they be tripped and the surplus pollen removed by washing with water. However, when all but three of the flowers on a raceme are removed, those intended for crossing can be reached more easily. The age of the flowers used as seed bearers for crossing seems to make little difference, provided they do not show signs of withering. It is perhaps the safer plan to select those flowers near the center of the raceme just when the buds at the end of the raceme are about to expand. The flowers should not be mutilated in any way, and of course should be handled as little as possible because of their delicate nature.

The first requisite consists in having pollen from the male parent at hand ready to be applied to the prepared stigmas. To do this most conveniently, as the flowers can not very well be manipulated with the fingers alone, it is desirable to have three pairs of forceps, one for each flower that is to be pollinated. Self-closing forceps are best, because they hold firmly the sexual column (Pl. III, *C* and *D*) used in pollinating. Take a flower from a raceme of the male parent, bend down and secure the banner between the tips of the thumb and the forefinger, then press with a pin or dissecting needle sidewise against the suture of the keel, beginning at the base and gradually drawing upward. If this operation is done carefully, the column will come out gently without disturbing the pollen from the anthers. When the flower has been tripped or exploded in this way, the terminal part comprising the stigma, with the masses of pollen surrounding the empty anthers closely arranged around it, hangs toward the operator free from contact with anything. With the aid of the self-closing forceps, sever the column from the flower, laying the columns aside ready to be applied to the stigmas of the flowers of the seed bearer when the latter is depollinated.

Now comes the most critical part of the operation, and the amount of skill with which it is performed determines the success or failure of the work. It must be understood that in the flower to be used as the seed bearer the stamens dehisced while the flower was in the bud stage, perhaps a day or two previously, and the pollen lies in masses all around the soft stigma (Pl. III, *C* and *D*), but still incompetent in that position to perform the acts of pollination and fertilization while the column is untripped. It should be the aim of the operator to trip the column in a manner that will cause a minimum disturbance of the arrangement of the pollen and prevent the terminal part of the column containing the sexual organs from springing with considerable force on the awaiting banner, thereby embedding a large number of its own pollen grains in the soft, pulpy stigma.

With this end in view, grasp one of the flowers gently but securely between the tips of the thumb and forefinger, with the back of the keel resting against the tip of the index finger. Cut an ordinary small-sized pin or needle in two, take the pointed end between the thumb and index finger of the free hand, place the half pin or needle against the lower part of the suture of the keel, and press gently against the keel, bringing the pin or needle up to the central part or a little beyond it, increasing the pressure gradually. This will compel the sexual column to alter its position, or "trip," gradually as the gentle pressure of the pin retards or prevents its springing with force enough to disturb the arrangement of the pollen grains around the stigma. Allow the pin supporting the sexual column to come gently toward the awaiting banner. It will then be found that, with the pin resting on the banner, the fingers may relax their hold, the pressure of the column toward the banner keeping the pin in place; and owing to the position of the pin, for the time being the terminal part of the sexual column, consisting of stigma and an abundance of pollen around it, is prevented from pressing on the standard, as it is about one thirty-second to one-sixteenth of an inch above it. (Pl. II, fig. 1, *C*, and Pl. II, fig. 2.) This gives the opportunity for the removal of the pollen grains by the use of a jet of water from the chip blower.

The action of the water effectually depollinates the flower without causing the least injury (Pl. II, fig. 1, *D*); in fact, the jet may be of sufficient force to remove even the empty anthers without injury to the stigma. (Pl. III, *E* and *F*.) However, the first few flowers operated on by the beginner should be examined before proceeding with the pollination to ascertain if the treatment given has been sufficient to depollinate the flower thoroughly.

After the jet of water has been applied there will be a considerable quantity of moisture covering the different parts of the flower, especially the empty anthers and stigma. This is immediately removed by touching these organs and other parts of the flower with a piece of blotting paper applied edgewise.

When this operation has been completed the exposed stigmas are pollinated in the following manner: Take one of the self-closing forceps, holding one of the previously prepared sexual columns from the flowers of the male parent, and with the stigma pointing upward push the end of the column containing stamens and freed pollen closely surrounding the stigma under the end of the column which has been depollinated, giving it a very slight circular movement to make certain that the large masses of pollen come in contact with the soft stigma of the depollinated flower. When this has been satisfactorily done, take hold of the supporting pin by the blunt end and gently withdraw it; the column then assumes its place on the banner with the stigma closely pressed against its surface (Pl. II, fig. 1, *F*), and a goodly number of pollen grains are embedded in the soft stigmatic surface. When the supply of pollen is unlimited a number of flowers may be tripped over a watch glass and the pollen applied to the stigma with a small brush, the hairs of which are held together with a weak sirup of sugar and water.

If the details described are carried out in a painstaking way, all that is done simply consists in substituting pollen from another variety for that which originally surrounded the stigma of the flower of the proposed seed bearer.

The operation is performed in much less time than it takes to describe it, and the operator is rewarded by a fairly high percentage of successful crosses. The first time the writer tried this method with two distinct varieties of *Medicago sativa* more than two-thirds of the flowers worked set seeds.

The second method of crossing alfalfa also involves depollination with the aid of a jet of water on the dehisced stamens, but it has now been discarded in favor of that just described. It is a simpler operation, requiring less delicate manipulation, but the percentage of successful crosses by it is very low. Besides, it involves the mutilation of the floral envelope and the exposure of the pollinated stigma to the atmosphere instead of allowing it to assume its natural position on the banner of the flower after being pollinated.

By this method all the flowers on a raceme may be used. First, by the aid of the scissors shown in figure 1, *A*, cut off all of the unopened buds and the banner of each flower left on the rachis. The reason for removing the banner is that when the flower column is tripped the position of the sexual column is altered so as to free it from contact with anything and to render it readily accessible.

The depollination of the flower thus becomes a very simple problem. The sexual column, being still imprisoned within the keel, is best tripped by a very light snip given by a pair of forceps, care being taken to place the tips of the forceps at a point near the base of the column so that the stamens and pistil are not interfered with in withdrawing. The sexual column being now free from the keel, the latter, together with the wings, should be cut off.

A small jet of water is then trained on the sexual organs from a water bulb or chip blower (see fig. 2, *A* and *B*); the stream should be quite gentle at first, followed with just sufficient force to remove both pollen and empty anthers. This will facilitate an easy approach to the stigmas when pollinating. Examine the stigmas with the aid of a lens to ascertain if all of the pollen has been removed; then remove the surplus water by applying lengthwise a piece of thick and very bibulous blotting paper. The flowers are now ready to be pollinated.

In preparing the sexual column of the pollen-bearing flower so that the pollen may be easily and quickly applied to the stigmas of the depollinated flowers of the seed bearer, detach one flower at a time and pollinate as described for the first method of crossing. If the pollinated stigmas are left exposed to the air, fertilization takes place only in a very small percentage of the flowers. They give a higher percentage when protected by a small paper bag, or each raceme may be placed inside of a test tube and kept in place by a small wad of cotton for twenty-four hours after pollination, the test tube being tied to a support and shaded from direct sunlight.

DEPOLLINATION BY COMPRESSED AIR.

The third method by which alfalfa and other flowers have been successfully depollinated is the use of compressed air. Contrary to expectation, this has no injurious effect on the tender parts of the pistil.

The parts of the flower are prepared in a manner similar to that described in the first method. The current of air is obtained from a small cylinder into which air is pumped to an indicated pressure of 20 pounds. The nozzle of the air tube is held about half an inch from the terminal part of the column by a helper; the full force is turned on just when the column is about to spring from the keel and is continued for ten or fifteen seconds after resting on the pin.

Pollination and subsequent treatment are performed in the same manner as given for the first method.

Fertilization following this method is satisfactory, but the percentage of successful crosses is not as high as in the first method described.

In depollinating large flowers of other genera having pistils that may be easily injured, it is very helpful to remove large quantities of pollen previous to the more thorough work by a jet of water from the chip blower.

THE GROWING OF THE PLANTS AND THEIR CARE.

In order to have the parent plants of alfalfa intended for crossing thoroughly under control, they should first be raised from seeds to ascertain if the varieties come true. The plants to be crossed should be grown in a cool greenhouse and when of sufficient size put in large pots, as then they are less apt to become suddenly dry at the roots. Good fibrous loam and a little rough sand make a good soil for pot culture. To prevent souring of the soil, place some large potsherds over the drainage hole, and over these place some half-rotted leaves. Ram the soil moderately firm around the roots, leaving sufficient space to give enough water at a time to last for two or three days.

It should be the aim of the cultivator to have the plants in bloom about the end of March or the beginning of April. At that season the absence of insects will render the work easier of accomplishment than when grown outdoors. Under outdoor conditions the plants would require to be protected by wire or cloth screens to exclude pollinating insects. Several specimens of each variety to be worked with should be grown to make certain of having some of them in bloom at the proper time. A strong plant of the variety to be used as the seed bearer should be selected.

RAISING LARGE QUANTITIES OF SEED FROM A CROSS.

When a promising variety of alfalfa has been secured by crossing, the problem of how best to secure a quantity of seed to sow a large area is undoubtedly a serious one. In the first place, the plants should be tested thoroughly to ascertain if they are superior to existing forms. The crosses obtained so far do not seem to vary much in the second and succeeding generations when seed is saved from flowers tripped by the hand. Those that prove of value from a single cross, the individuals of which are evidently alike, should be propagated vegetatively and the progeny of each plant kept separate till planted out in the field, when they may be mixed for cross-pollination. The cuttings will root satisfactorily in a cold frame if kept closed for a few days. It is possible by this method to root several hundred cuttings during the summer, beginning with a single mother plant in the spring, but it must be understood that these cuttings originating from a single mother are to be considered as one plant; that is, if seeds set poorly on the mother plant as a result of self-pollination by artificial tripping, all the plants propagated asexually from the original will have the same peculiarity. If the asexually propagated progeny be planted in a field a safe distance from other varieties, the probabilities are that the plants from the resulting seed will come true and the strain be established. In this way a much larger crop of seed can be secured in a given time than if one depends altogether upon seeding the original individuals of a cross.

CROSSING LARGE-FLOWERED LEGUMES.

In crossing varieties of legumes which come true from seed resulting from self-pollination, it is not necessary to work with a large number of flowers. Careful manipulation of a few will give all the possible results with any two varieties, and usually the operator will get more varieties than he desires in the second and subsequent generations. The flowers of such plants as Phaseolus, Stizolobium, Vigna (Pl. IV, fig. 1), Pisum, and Lathyrus should be emasculated in the bud stage and before the anthers shed their pollen. The operator before under-taking to cross two varieties should have a perfect knowledge of the parts of the flower.

The idea of having large models of the various flowers of the principal garden and field crops in agricultural colleges and schools is a good one. It enables prospective plant breeders to become familiar with the structure of the common flowers and shows what is necessary to be done in preparing flowers for crossing more quickly than the study of the flowers themselves or the use of illustrations made by others. Many of the flowers of forage plants and vegetables are so minute that it is with difficulty that they are emasculated even with the aid of a good dissecting microscope. This is the case with all the species of Melilotus and a goodly number of the species of Medicago and Trifolium; and the student, having the forms and structure of the flowers continually in his mind, will be better prepared to cope successfully with plant-breeding problems.

Among the large-flowered legumes, varieties of which it is desired to cross, the cowpea may be chosen as a good example in order to show how the flower is manipulated previous to pollinating. In the evening it is found that the buds which will expand the next morning are quite large and easily manipulated in emasculating. (Pl. IV, fig. 1, *A*.) Hold the bud between the thumb and the forefinger, with the keeled side uppermost (Pl. IV, fig. 1, *B*); then run a needle along the ridge where the two edges of the standard unite. Bring down one side of the standard, securing it in position with the thumb; then do the same with one of the wings, which will leave the keel exposed. This must be slit on the exposed side about one-eighth of an inch below the bend in the keel and continuing along until about one-sixteenth of an inch from the stigma, which can be seen through the tissue of the keel. Bring down the section of keel and secure it under the end of the thumb. This will expose the immature stamens, 10 in number. (Pl. IV, fig. 1, *B*.) With a fine-pointed pair of forceps seize the filaments of the stamens and pull them out, counting them as they are removed to make certain that none are left. (Pl. IV, fig. 1, *C*.) Allow the disturbed parts of keel, wings, and standard to assume their original positions as far as possible. Next detach a leaflet from the plant, fold it once, place it over the emasculated flower bud, and secure it in position with a pin or toothpick. This will prevent the bud from drying out before the stigma matures sufficiently to be pollinated from a flower of a different variety next morning. If the stamens are removed without altering the position of the pistil (Pl. IV, fig. 1, *C*) or injuring it in any way and pollen is applied the morning after the flower is emasculated (Pl. IV, fig. 1, *D*), in nine cases out of ten they will set seed; and if none of the anthers were ruptured in their removal, the resulting seedlings will have some of the characters of both parents. If the two parents have spotted seeds and the seed bearer, for instance, be the well-known variety New Era (Pl. IV, fig. 2, *A*) and the pollen bearer the equally well-known Whippoorwill variety (Pl. IV, fig. 2, *B*), the seeds resulting from the first-generation plants will have the markings of both parents on each seed, giving a beautiful example of crossing in the seed itself. (Pl. IV, fig. 2, *C*.) In the second generation we have a strange combination. About nine parts of the resulting seeds are like those of the first generation, three parts like Whippoorwill, three parts like New Era, and one part self-colored, resembling the lighter or ground color of the straight Whippoorwill seeds; but in the first three lots, although the series are easily classed, there are upward of 30 variations in color alone, and many more when we take form and size into consideration. In subsequent generations they again vary until by following defined rules we get new fixed types.

However, the variations in cowpea crosses are not always so very apparent, especially when two varieties having seeds of the same color are selected as parents. While there are great differences in the other characters of the progeny, such as foliage, early and late ripening, vining habit, upright growth, and disease resistance, the seeds differ from the parents and among themselves apparently only in size and shape; and while in the first-mentioned cross one could pick out dozens of dissimilar seeds in the colors alone, three or four variations in size and shape are about all that the operator may expect from crossing varieties the seeds of which are similar in color but vary in size.

In the condition of the mother plant at the time of pollination there is fortunately some choice which makes for a high percentage of successful pollinations. It will be found, especially with the cowpea, that young plants allowed to fruit in 5-inch pots set seed with greater certainty than will rampant-growing plants in large pots. Again, old plants in large pots break freely into growth, but not of a viny nature. This growth produces flowers in abundance, and pods form with great freedom either from their own pollen or when crossed with pollen from other varieties.

CROSSING IN LARGE AND SMALL NUMBERS.

A matter of importance in plant breeding and one which does not receive the attention it deserves from the practical breeder is the grouping of varieties into at least two classes for somewhat different treatment in crossing. In the first division all the plants we now call varieties, which come true from seed, no matter how they originated, may be termed artificial species. This division includes garden and field crops, such as lettuce, cabbage, and turnips; radishes and others of this family; onions and other plants of the same natural order; carrots, celery, parsley, and parsnips; the cereals; varieties of alfalfa, and many others which come true from seed and are only propagated sexually. With these there is no necessity for raising many individuals of the first generation. If the breeder succeeds in getting a desirable cross between two well-defined kinds, a few individuals of the first generation are enough, provided the work of emasculation or depollination and the application of pollen to the flower so treated is not carried out in a perfunctory manner. The individuals of the second generation, if they are sufficiently numerous, will give the variations from which to choose selections for perpetuating.

The second great division includes those plants which do not come true from seed or at least have never been bred to reproduce in that manner. The treatment in crossing is different from that which should be accorded the sexually propagated varieties, in that large numbers of the first generation are necessary, so that the chances of securing improved forms will be greater in proportion to the number of seedlings raised from any one cross. Nearly all fruit and nut trees, grapevines, bush fruits, strawberries, and potatoes are included in this class; also many florists' flowers, such as roses, carnations, gladiolus, dahlia, fuchsia, chrysanthemums, and pelargonium. When the desired improvement is attained by crossing any two varieties, one plant of the improved form is sufficient to start with, and that is increased vegetatively, i. e., by cuttings, budding and grafting, layers, bulblets, cormlets, etc.

In this second division, when breeding improved forms by crossing is attempted we look for results in the first generation; consequently, the number of flowers pollinated must be large, so that the seed ripened will be in quantities large enough to give the necessary variation in the resulting seedlings. The plants mentioned above which are propagated asexually are all hybrids, crosses, or sports which have never been bred sufficiently to come true from seed; thus, when any two plants of distinct varieties are crossed we never can tell exactly what the progeny will be like, and it is as a rule so very varied that if we get one seedling in five thousand possessing characters superior to either parent we are doing well.

HYBRIDIZING SPECIES.

HELIANTHUS HYBRIDS.

It may be necessary at times to hybridize two natural species. If a hybrid is raised, the probabilities are that it will not set seed with its own pollen. This was the case in a hybrid recently raised between *Helianthus argophyllus* and *H. debilis*, the latter being the pollen-bearing parent. The plants, although subjected to the best treatment, did not set a single seed from their own pollen or from pollen applied from one flower head to the stigmas of another on the same plant; nor was a single seed set on a plant the flowers of which were pollinated with pollen taken from flowers on separate plants; but when a flower of the hybrid was pollinated with pollen from the male parent, seeds were produced freely. These when sown and the plants put in the open ground also seeded very abundantly; the flowers resulting from these seedlings were much finer than those of the parents or any of their forms. It remains to be seen, however, just how the third generation will turn out, as in the seedlings of this generation, now only a few inches high, the variation of the foliage is considerable.

GRASS HYBRIDS.

In hybridizing two species of grass lately the results obtained would indicate, in this instance at least, that large numbers of hybrid seedlings are not necessary in the first generation of grass hybrids. Out of 13 seeds secured, 10 germinated, and no two plants are alike; in fact, the variation in the progeny of the first generation is more marked than in any second-generation seedlings of any other cross between two varieties with which the writer is familiar. The parents were *Poa arachnifera* and *P. pratensis*, the latter being the pollen bearer. The seed bearer was a hermaphrodite plant and the only one out of about 400 seedlings.

The flowers of the seed bearer were thoroughly treated with water each morning until the crop of stamens was exhausted. A very large quantity of pollen from *Poa pratensis* was secured by cutting half an armful of culms of *P. pratensis* when in bloom; these were put in a vessel of water in the evening. Next morning the stigmas of *P. arachnifera* were thoroughly pollinated by taking one handful at a time of the culms of *P. pratensis* and shaking them over the depollinated stigmas of the Texas bluegrass. This was done in a greenhouse; the stigmas were almost hidden by the pollen. Only 13 seeds resulted, but these were more than enough, as each of the progeny might well have been taken for a new species.

Each of the 10 seedlings was propagated by division and 100 plants of each put out in the field. No seeds were produced, as the pollen was imperfect; not a single grain was found in good condition.

Pollen from *Poa pratensis* was again applied in 1908, and the plants seeded abundantly. The resulting seedlings are exceedingly varied. Some have long, broad leaves; others short and broad, narrow and short, or narrow and long leaves.

CROSSING CULTIVATED VARIETIES ON NATURAL SPECIES.

PANSIES.

To show what might be expected in renewing the vigor of some varieties by crossing them on wild progenitors, it may be permissible to mention some work in the improvement of the common pansy in an attempt to enable it to better withstand our hot summers. Some time ago a number of plants of *Viola tricolor* were found growing luxuriantly in southern California in hot and dry places. Even far down in the Imperial Valley, where the temperature frequently reaches a stage unheard of in the East, the plants seemed at home.

The idea suggested itself that this plant might be of use in imparting heat-resistant characters to the cultivated pansies. Plants were raised from the seed gathered and pollen from a strain of pansies applied to the stigmas of the wild plants. Some of the flowers of the first-generation progeny are shown in Plate XIV. The petals were removed from the flowers of the wild plant and their stigmas cleared of pollen with the aid of water previous to pollinating. All the plants secured have fair-sized flowers, more or less resembling in color and markings those of the wild type. The foliage more closely resembles the mother than it does the father. Recrossing with pollen from a good strain the present season will probably give the desired size next season.

DAHLIAS.

The original Twentieth Century dahlia was used in pollinating a new species from Mexico four years ago. This species has very small, bright-red flowers, and the stems are exceedingly long. The larger and very rough leaves are produced near the crown of the plant, leaving the principal stems with only very small leaves. The flowers of the Mexican plant were depollinated (Pl. V, figs. 1 and 2) and pollen applied to three of the flowers. Sixteen seedlings resulted; the small number of seeds was probably due to the fact that the mother plants were growing in small pots in the greenhouse and did not flower till after the outdoor crop had been blackened by frost. The pollen was obtained from flowers which had been saved and kept in water.

The resulting first-generation seedlings were strictly intermediate between the parents, all of them with very long stems (see Pl. XV), but the varieties were not striking enough in color or size of flower to warrant vegetative propagation. The best of them were bagged and allowed to set seeds. The seedlings of the following season gave a very large assortment of forms, and the colors were more varied than those of the first generation. About fifty forms were saved for further crossing and selection. The following summer the best of these were crossed with pollen from the cactus and other varieties. As a result a few crosses were produced which show that varieties may be raised in this way with large and well-formed flowers, some of them equal in these respects to some of our best varieties bred from plants in cultivation for nearly a century. One of the forms with single flowers is shown in Plate XV.

CROSS-POLLINATING CLOVERS.

To pollinate clover flowers artificially may seem a difficult operation on account of their minute and delicate structure, but in reality it is even more simple than the manipulation of the flowers of alfalfa. Many observations indicate that the flowers of the red clover are incapable of self-fertilization when protected from insects, as plants which have been tested with this end in view have in no case produced seeds. It would, however, seem that the emasculation of clover flowers is unnecessary, because when the keel is pulled forward and the stamens disturbed it rarely happens that the pollen comes in contact with the stigma.

When it is desired to perpetuate well-defined varieties by careful intercrossing of individuals,. the work of transferring pollen from the anthers of one plant to the stigmas of another can be rapidly and effectively performed in the following manner: Select plants of both the proposed pollen and seed bearers which have developed flowers under the protection of a wire screen. We can then be reasonably certain of the absence of insect interference. Take a flower of the pollen bearer between the thumb and forefinger of the left hand, and using the forceps having a flattened pin tied to one end, as shown in figure 1, *C*, place the flat side of the pin parallel with the standard of a floret, the pin pointing to the base of the keel, and draw it gently upward. The result will be that many grains of pollen will adhere to the flattened portion of the pin. Turn the forceps in the hand so that the prongs take the position first held by the pin. This must be done carefully so as not to dislodge the pollen on the end of the pin. Then with the prongs of the forceps snip a piece from the end of the banner of the flower intended to be pollinated. This will show which of the flowers on a head have been manipulated. Next take one of the prongs of the forceps and bend down the keel and wings of the floret to be pollinated, securing them in a position under the end of the thumb. This operation will bring the upper part of the pistil into view. The forceps are now turned in the hand to their first position and the pollen carefully applied to the stigma. The operation is concluded by restoring the keel and wings to their original positions.

METHODS OF EMASCULATING AND POLLINATING COMMON FLOWERS.

THE ESSENTIAL ORGANS OF THE FLOWER.

In the greater number of flowering plants there are what are usually termed male and female organs in each flower. The rose (Pl. XI, figs. 1 and 2) and canna (Pl. IX, fig. 2, *A*, *B*, and *C*) are familiar examples. These are called hermaphrodite flowers.

Other plants have the male and female organs in separate flowers, but on the same plant, as in the begonias (Pl. XII, fig. 1) and the genus Codiaeum (Pl. XII, fig. 2). Flowers of this nature are termed monœcious.

There is still another class of plants which has the male flowers on one plant and the female flowers on another. Examples of this arrangement are found in the willows (Pl. XIII, fig. 1), the aucuba, the genus Nepenthes, and commonly in the edible asparagus (Pl. XIII, fig. 2). These flowers are termed diœcious.

The so-called male organs are the stamens (Pl. XI, fig. 1, *Sta*), usually consisting of the filaments, or stalks, and the anthers containing the powdery material, or pollen. The so-called female organ is the pistil (Pl. XI, fig. 1, *P*). The lower part is the ovary (Pl. IX, fig. 2, *a*, *o*); the next part, in some flowers absent, is known as the style (Pl. III, *E* and *F*). The terminal part, that on which the pollen is deposited, is the stigma (Pl. III, *E* and *F;* Pl. IX, fig. 2, *S*).

PREPARATION OF FLOWERS TO BE POLLINATED.

In crossing plants which have both male and female organs present in the same flower (Pl. XI, fig. 1) the principal point to be kept in view is the removal of the anthers from the flower which is chosen as the seed bearer before the pollen is ripe; this is to prevent self-pollination of the flower. It is also necessary to prevent pollen from other flowers on the same plant or from flowers on other plants of the same variety or species gaining access to the stigma of the flower to be cross-pollinated. To this end it is always advisable to have isolated plants for seed bearers.

A few of the flowers or as many as can be conveniently worked at one time may be selected for crossing, and the others removed. The selected flowers should be covered with paper bags, or, better still, the whole plant if not too large may be covered with a small-mesh wire screen, which will effectually prevent pollination by winged insects.

In some plants the anthers of the flower intended to be used as the seed bearer must be removed when the flower is in the bud stage, as the stamens mature long before the pistil (see Pl. X, fig. 2). This operation in many cases necessitates the mutilation of the petals; therefore, emasculation in the bud stage should never be performed except in those cases where the anthers shed their pollen before the petals expand. Many plants shed their pollen only after the petals expand, as in the rose and the lily, and this is the safest time to remove the anthers provided the flowers have been protected against access of pollen to the stigmas.

In plants like *Tecoma grandiflora* the anthers dehisce long before the flower opens, but the lobes of the stigma are closed and do not open until the anthers of the same flower have shriveled. However, the pollen grains which lie in the tube of the flower might be brought into contact with the stigma; therefore, it is safest to remove the anthers before they open.

With some plants, such as the anthuriums, the stigmas are ripe several days before the pollen matures. In this case the anthers can not be removed, nor is there any necessity for their removal in crossing. The common plantain (*Plantago lanceolata*) (Pl. X, fig. 1) is another plant in which the pistil matures a short time before the stamens of the same flower, thus insuring cross-pollination.

Those plants which have the stigmas and the stamens in separate flowers on the same plant, as in the genus Begonia and the genus Codiaeum (Pl. XII, figs. 1 and 2), should have the staminate flowers removed before they open and the pistillate flowers inclosed in small manila paper bags both before and after pollination, or if the proposed seed bearers are growing in pots they should be isolated and screened.

With plants which have pistillate flowers on one plant and staminate ones on another, as in the genus Nepenthes, willows (Pl. XIII, fig. 1), and asparagus (Pl. XIII, fig. 2), it is only necessary to guard against undesirable pollen by bagging the flowers before and after pollination.

REMOVAL OF THE ANTHERS.

The removal of the anthers in the case of flowers having both stamens and pistils is called emasculation. There are various ways in which the anthers may be removed. Perhaps the best method is to use the forceps shown in figure 1, *C*, as the most delicate stamens may be seized and their anthers removed with this instrument. When all the stamens are visible to the eye the process is an easy one. When, however, the operator wishes to emasculate a flower of a legume (Pl. IV, fig. 1) or of any other plant in the bud stage, he should know the number of stamens in the flower of each species, and the anthers should be counted as they are removed, thus making certain of the complete emasculation of the flower.

SECURING POLLEN.

To have the pollen of a flower to be used in pollinating absolutely pure, it is necessary that the stamens be protected, both before and after dehiscing, by the use of paper bags. To secure pollen in sufficient quantity to make certain that the stigmas of the proposed seed bearer are well covered, the best method is to secure a few flowers just before the anthers open, with stems long enough to go into a vessel of water. Let the vessel containing the flowers stand indoors until the stamens dehisce; then hold that part of the flower on which the stamens are situated over a watch glass and gently agitate the stamens with a pin. The pollen from a few flowers—of the rose, for instance (Pl. XI, fig. 2, *A*)—will fall in sufficient quantity to cover the glass. Then place the glass in a small box so that it may safely be carried from place to place. Some flowers have pollen which can not well be treated in this manner because it clings together in masses, as in the cowpea and the lily.

APPLYING THE POLLEN TO THE STIGMA.

In those flowers having pollen which clings together and adheres to the stamens the pollen is best applied to the stigmas directly from the stamens by means of the flattened pin shown in figure 1, *C*. Pollen such as that of the rose should never be applied with a dry brush unless there is a large quantity available, as this method means the loss of a very large percentage of the grains. In carrying the pollen from the glass to the stigma the least jar or movement of the air causes it to fall from the brush.

The most satisfactory method of transferring dry pollen is to use a very small brush prepared in the following manner: Dip the hairs in a weak sirup of sugar and water, draw them between the finger and thumb to remove the surplus moisture and to flatten the mass of hair, clip off a small portion of the ends so that the hairs will be all of one length, and trim the sides, which will result in the hairs sticking together. While still damp push the end of the flattened brush among the pollen grains, and even the driest pollen will adhere in masses. It is thus abundantly and easily applied to the most delicate stigmas. The experienced breeder can tell at a glance when the stigma of any flower is ready to be pollinated. The stigmas of the rose shortly after the petals expand indicate the receptive condition, and this may be taken as a guide for the stigmas of most flowers.

DESCRIPTION OF PLATES.

Plate I. Fig. 1.—Staminal tubes and stigmas of lettuce flowers (enlarged 20 diameters): *A*, Staminal tube; *B*, stigma appearing through end of tube; *C*, stigma covered with pollen; *D*, stigma depollinated. Fig. 2.—Depollinating lettuce flowers with water from a garden hose.

Plate II. Fig. 1.—Flowers of alfalfa (enlarged 5 diameters), showing the method of depollinating and crossing used: *A*, Untripped and unpollinated flower; *B*, tripped and self-pollinated flower; *C*, flower showing sexual column tripped against a pin, to prevent self-pollination and to provide the opportunity for depollination; *D*, depollinated flower; the operation is performed by training a jet of water on the sexual organs while the column is resting on the pin; *E*, flower showing the stigma pollinated with pollen from the flower of a distinct variety or species while the column is still resting on the pin; *F*, flower from which the pin has been withdrawn after pollination, allowing the stigma to press against the surface of the banner. Fig. 2.—Raceme of alfalfa flowers (enlarged 6 diameters). This illustration shows that when the column of the flower is tripped the pressure is sufficient to hold a small pin.

Plate III. Sexual columns of alfalfa flowers (enlarged 10 diameters), showing different stages of development: *A* and *B*, Columns with anthers just before the dehiscing stage; *C* and *D*, columns with anthers dehisced; *E* and *F*, columns with pollen and empty anthers removed by the aid of water previous to artificial pollination.

Plate IV. Fig. 1.—Flowers and young pods of the cowpea (twice natural size): *A*, Flower bud showing condition on the evening of the day previous to the opening of the flower; *B*, flower in the bud stage, showing how the floral envelope is opened to gain access to the stamens for emasculation; *C*, flower with stamens removed, showing the large stigma to the left; *D*, emasculated flower the next morning after pollination; *E*, young pod the second morning, showing that fertilization has been accomplished; *F*, the same pod forty-eight hours after the pollination of the flower. Fig. 2.—Seeds of cowpea parents and of a first-generation cross (enlarged 2½ diameters). *A*, New Era; *B*, Whippoorwill; *C*, New Era ♀ × Whippoorwill ♂.

Plate V. Fig. 1.—*Dahlia chisolmii* (enlarged 4 diameters), showing disk florets before depollination. The stigmas are densely covered with pollen. Fig. 2.—*Dahlia chisolmii* (enlarged 4 diameters), showing disk florets after depollination by a jet of water.

Plate VI. Fig. 1.—Disk florets of the greenhouse cineraria before depollination (enlarged 5 diameters), showing the stigmas covered with pollen. Fig. 2.—Disk florets of the greenhouse cineraria (enlarged 5 diameters) after depollination with water.

Plate VII. Fig. 1.—Flower of dahlia (enlarged 5 diameters), showing the disk florets, the stigmas of which are nearly all covered with pollen. The stigmas of the inner florets are not fully developed. On these the pollen is very abundant. Fig. 2.—The dahlia flower (enlarged 5 diameters) shown in figure 1, with the outer florets depollinated by a jet of water. The stigmas of the inner florets are not fully developed.

Plate VIII. Fig. 1.—Dahlia florets (enlarged 10 diameters), showing development of the stigmas: *A*, Unopened disk floret; *B*, floret after the staminal tube enveloping the stigma has appeared above the corolla; *C*, floret with the stigma partly protruding from the staminal tube; at this stage it is thickly covered with pollen; *D*, floret with the stigma still farther advanced; the upper part of the staminal tube is seen near the base of the stigma; *E*, floret with the stigma fully developed and covered with pollen; *F*, floret with the stigma depollinated with water. Fig. 2.—Dahlia florets (enlarged 6 diameters), before and after depollination: *A*, Disk florets, showing the stigmas covered with pollen; the staminal tubes have been pulled within the corollas; *B*, florets with the stigmas depollinated by water.

Plate IX. Fig. 1.—Disk florets of Helianthus (enlarged 5 diameters), showing different stages of development: *A*, Floret in bud stage; *B*, floret, showing staminal tube inclosing stigma, the upper part covered with pollen; *C*, floret (twenty-four hours later), showing the stigma covered with pollen and the staminal tube partly drawn within the corolla; *D*, floret with the stigma depollinated; this is done when the floret has reached the stage shown in *B*. Fig. 2.—Flowers of *Canna indica* (natural size), showing stamen and pistil in different stages of development. *Sta*, Stamen; *S*, stigma; *O*, ovary.

Plate X. Fig. 1.—Flowers (proterogynous) of *Plantago lanceolata*, showing pistils maturing before the stamens: *A*, Flower head, showing mature pistils; *B*, flower head, showing a few stamens to the right; C, flower head, showing withered stamens at the base of the flower spike; *D*, flower head in a more advanced stage. Fig. 2.—Flower (proterandrous) of *Campanula rotundifolia* (enlarged 3 diameters), showing stamens maturing before the pistil. *A*, Flower bud; *B*, flower bud with corolla removed, showing large, mature stamens encircling the immature pistil; *C*, flower with portion of corolla removed; the stigma is still immature, the anthers have discharged their pollen, and the stamens are wilted and curled around the base of the style; *D*, flower after the corolla has withered and the stigma has expanded.

Plate XI. Fig. 1.—Single tea rose, showing how easily hermaphrodite flowers having large stamens may be emasculated: *Sta*, Stamens; *P*, pistils. Fig. 2.—Flowers of roses (natural size), showing method of emasculation: *A*, Flowers with petals removed, showing stamens and pistils; *B*, flowers with stamens removed, showing stigmas ready to be pollinated.

Plate XII. Fig. 1.—Flowers (monœcious) of begonia, showing the sexes in different flowers on the same plant: *A*, *A*, Pistillate flowers; *B*, *B*, staminate flowers. Fig. 2.—Staminate and pistillate flowers of *Codiaeum variegatum* from the same plant. *A*, Male flowers; *B*, female flowers.

Plate XIII. Fig. 1.—Staminate and pistillate (diœcious) flowers of willow from different plants: *A*, Female flowers; *B*, male flowers. Fig. 2.—Flowers from staminate and pistillate plants of *Asparagus officinalis* (enlarged 5 diameters): *A*, Pistillate flowers; *B*, staminate flowers.

Plate XIV. Flowers from first-generation seedlings of crosses of pansies (natural size). *Viola tricolor* ♀ × cultivated forms ♂. The row of flowers at the bottom is *V. tricolor* uncultivated.

Plate XV. Single branch of hybrid dahlia plant. *Dahlia chisolmii* ♀ × Twentieth Century dahlia ♂. Height of branch 7 feet 6 inches, showing very large compound leaves near the base and long flowering stems.

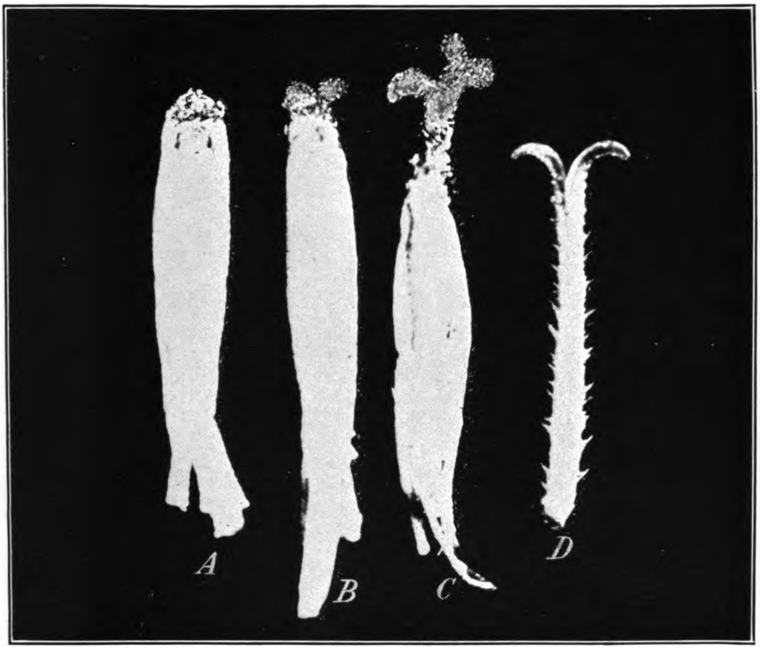


FIG. 1.—STAMINAL TUBES AND STIGMAS OF LETTUCE FLOWERS (ENLARGED TWENTY DIAMETERS).

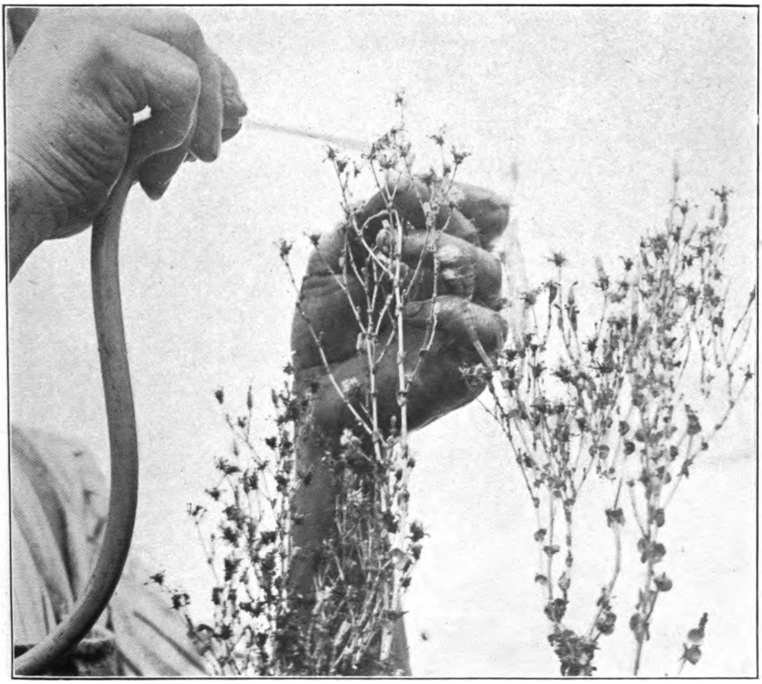


FIG. 2.—DEPOLLINATING LETTUCE FLOWERS WITH WATER FROM A GARDEN HOSE.

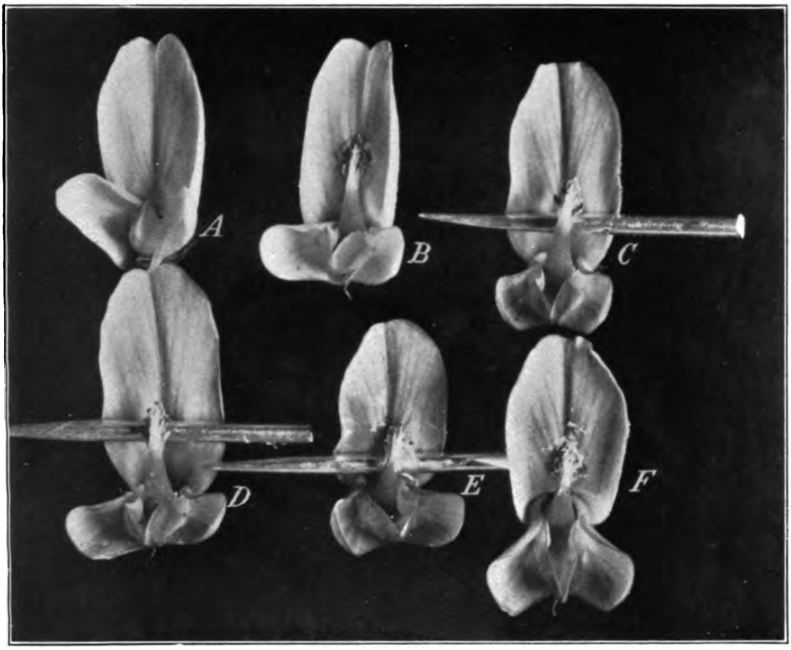


FIG. 1.—FLOWERS OF ALFALFA (ENLARGED FIVE DIAMETERS), SHOWING THE METHOD OF DEPOLLINATING AND CROSSING USED.

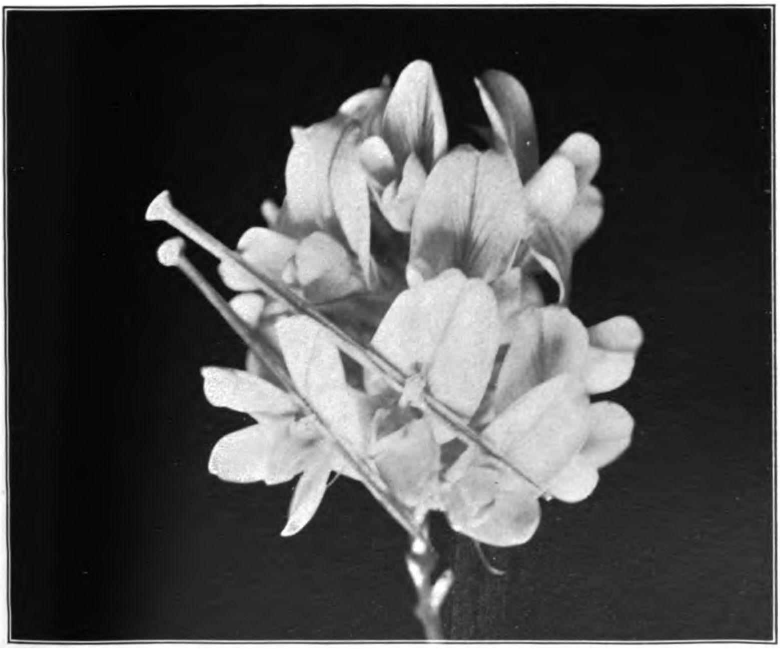
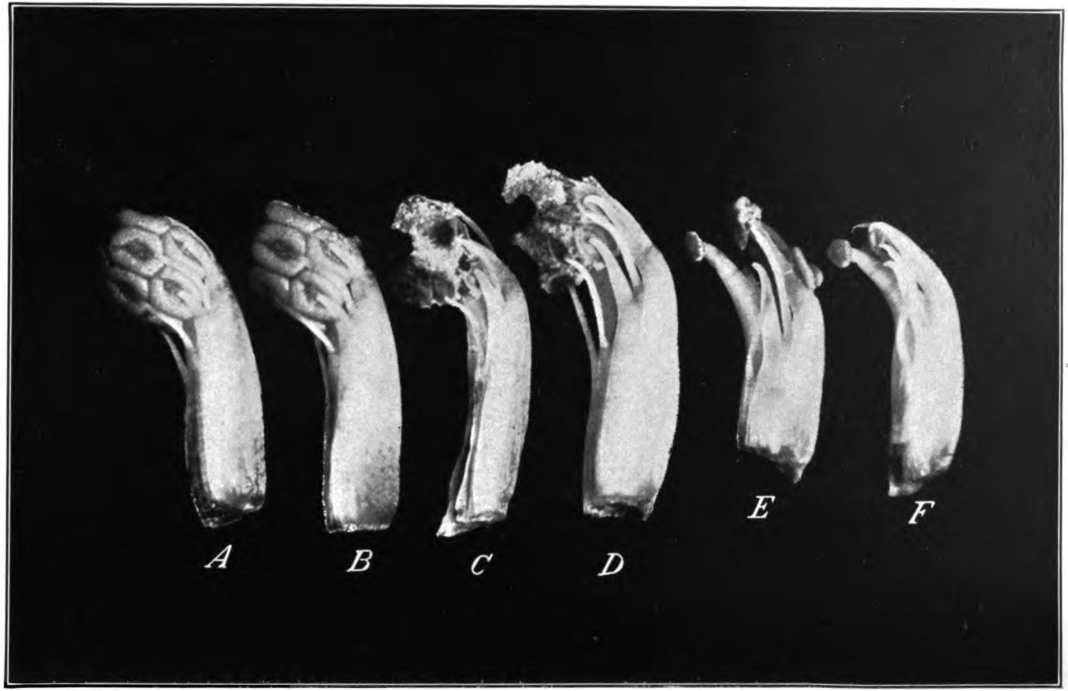


FIG. 2.—RACEME OF ALFALFA FLOWERS (ENLARGED SIX DIAMETERS).

PLATE III.



SEXUAL COLUMNS OF ALFALFA FLOWERS (ENLARGED TEN DIAMETERS), SHOWING DIFFERENT STAGES OF DEVELOPMENT.

A and *B*, Columns with anthers just before the dehiscing stage; *C* and *D*, columns with anthers dehisced; *E* and *F*, columns with pollen and empty anthers removed by the aid of water previous to artificial pollination.

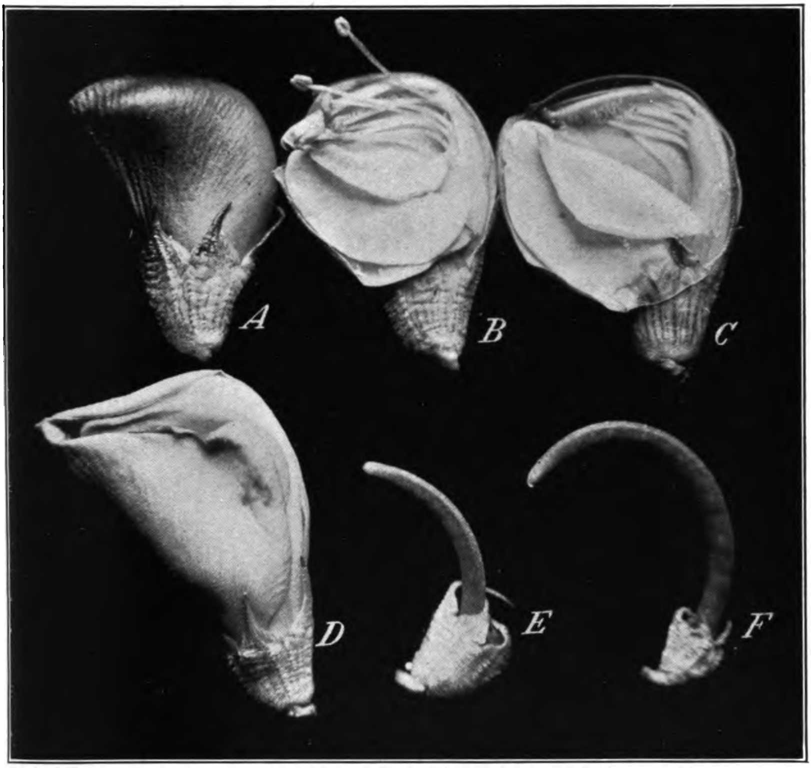


FIG. 1.—FLOWERS AND YOUNG PODS OF THE COWPEA (TWICE NATURAL SIZE).

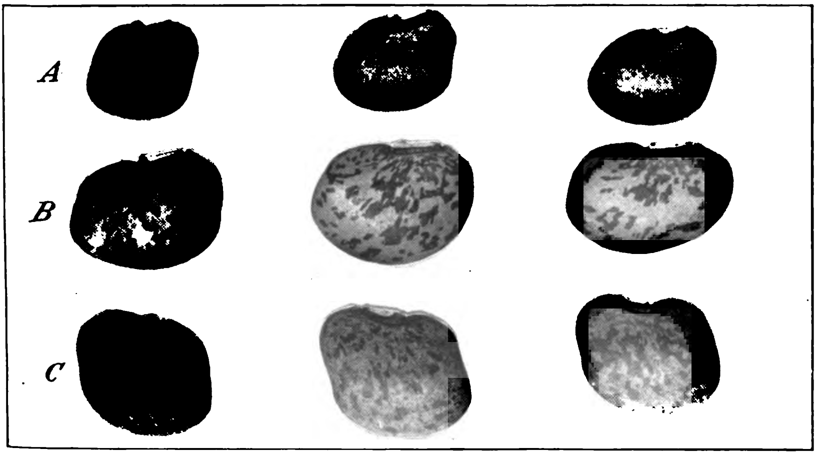


FIG. 2.—SEEDS OF COWPEA PARENTS AND OF A FIRST-GENERATION CROSS (ENLARGED TWO AND ONE-HALF DIAMETERS).

A, New Era; *B*, Whippoorwill; *C*, New Era ♀ × Whippoorwill ♂.

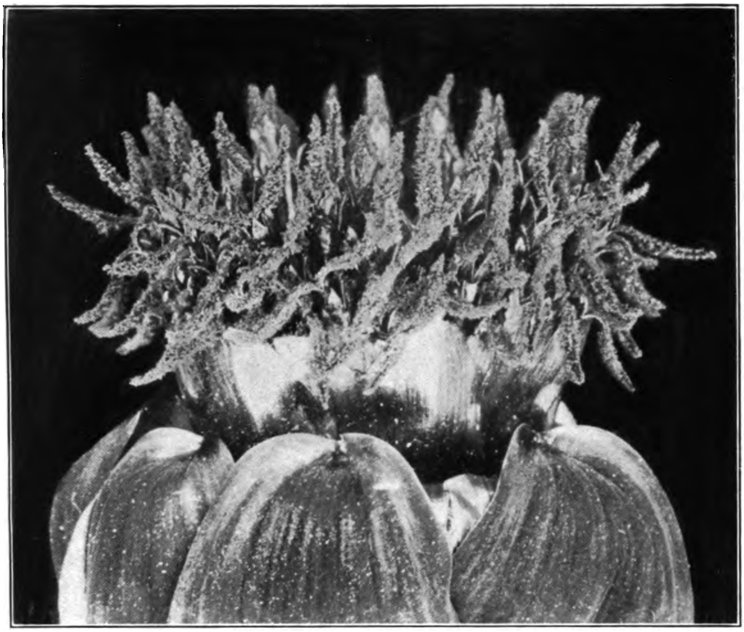


FIG. 1.—DAHLIA CHISOLMII (ENLARGED FOUR DIAMETERS), SHOWING DISK FLORETS BEFORE DEPOLLINATION.

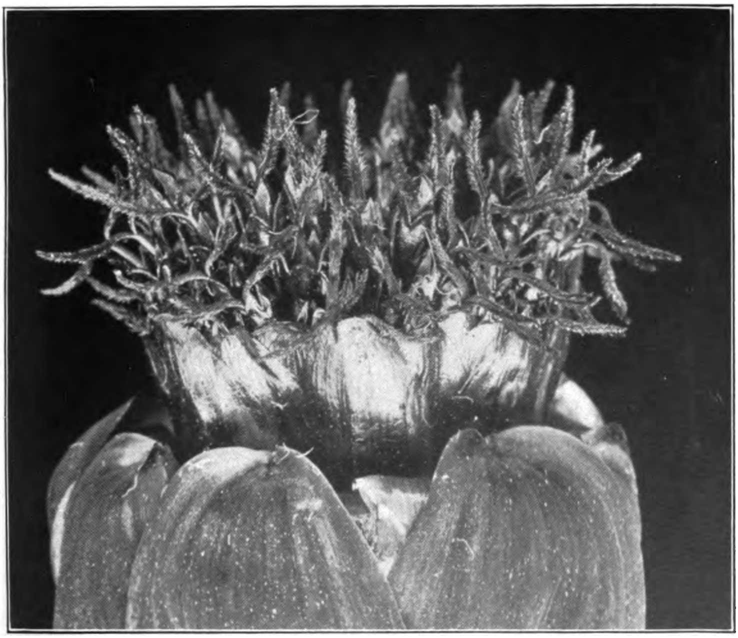


FIG. 2.—DAHLIA CHISOLMII (ENLARGED FOUR DIAMETERS), SHOWING DISK FLORETS AFTER DEPOLLINATION BY A JET OF WATER.

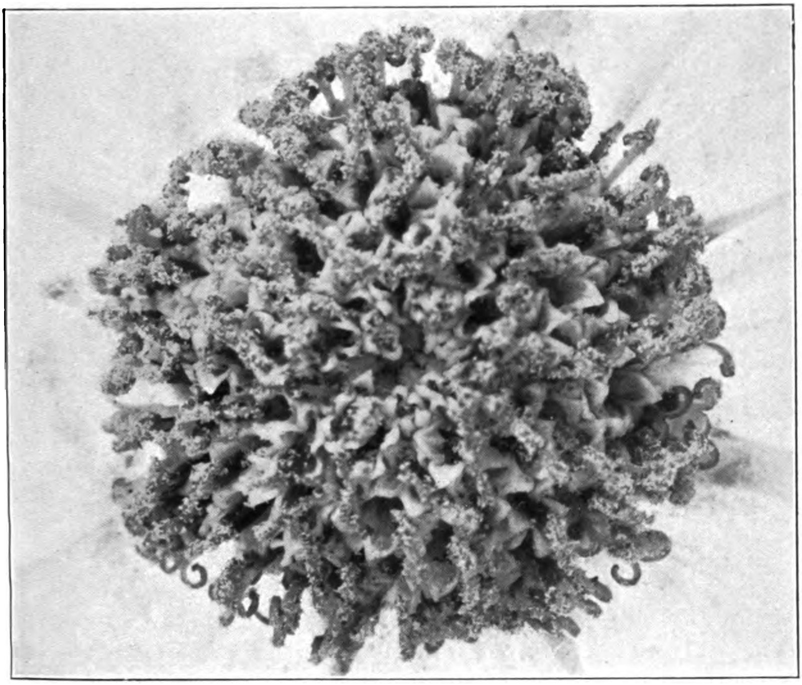


FIG. 1.—DISK FLORETS OF THE GREENHOUSE CINERARIA BEFORE DEPOLLINATION (ENLARGED FIVE DIAMETERS).

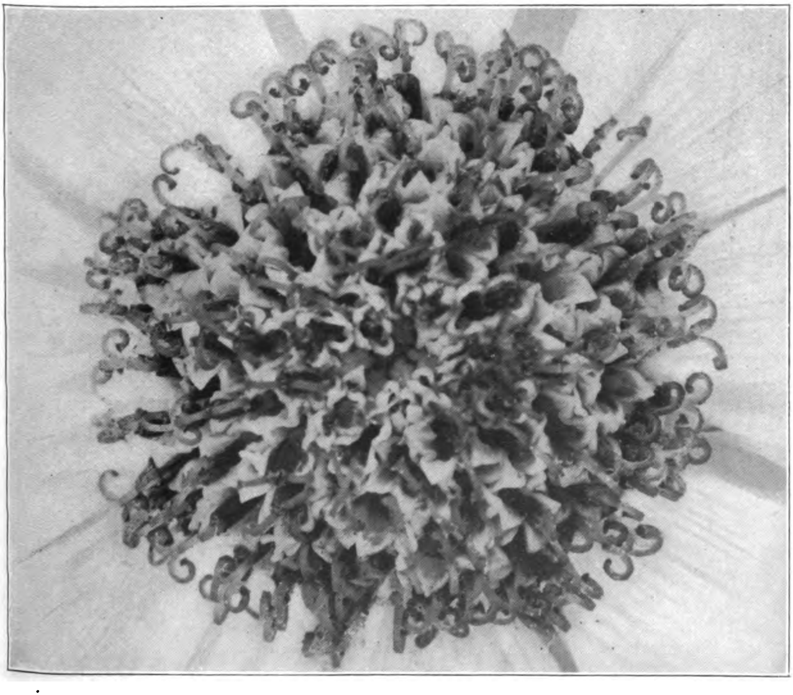


FIG. 2.—DISK FLORETS OF THE GREENHOUSE CINERARIA AFTER DEPOLLINATION (ENLARGED FIVE DIAMETERS).

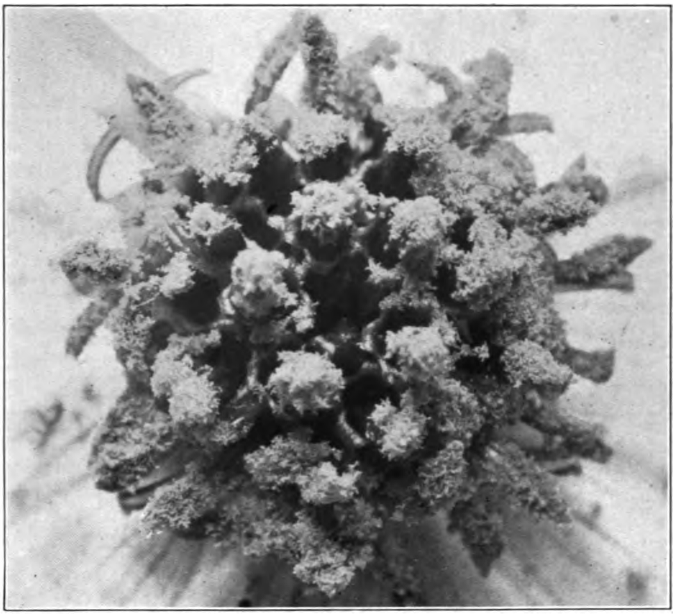


FIG. 1.—FLOWER OF DAHLIA (ENLARGED FIVE DIAMETERS), SHOWING THE DISK FLORETS, THE STIGMAS OF WHICH ARE NEARLY ALL COVERED WITH POLLEN.

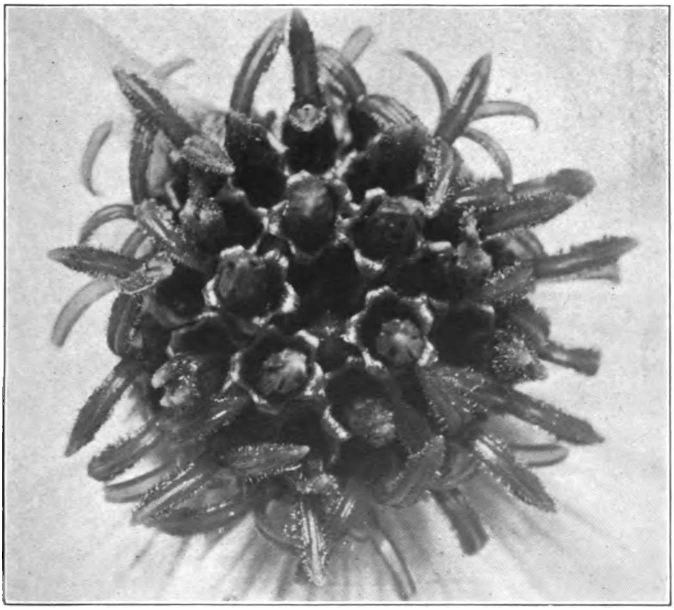


FIG. 2.—THE DAHLIA FLOWER (ENLARGED FIVE DIAMETERS) SHOWN IN FIGURE 1, WITH THE OUTER FLORETS DEPOLLINATED BY A JET OF WATER.

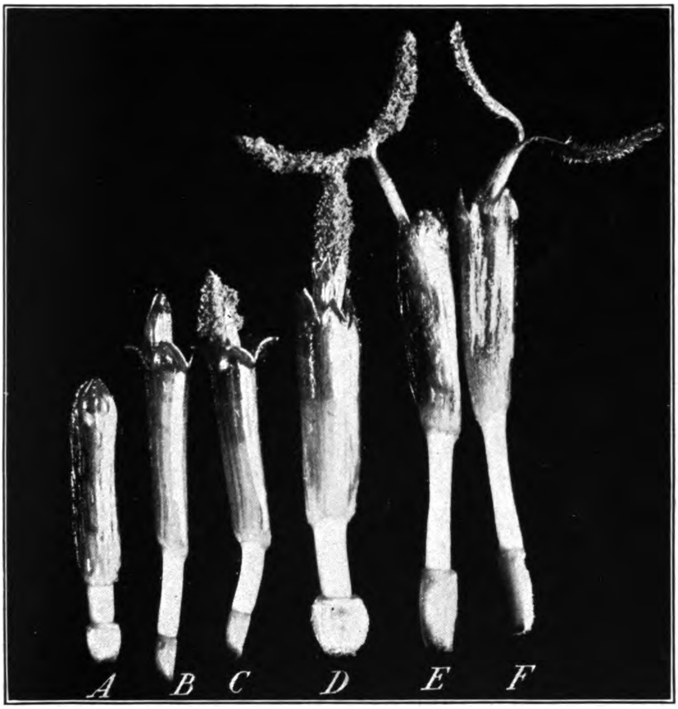


FIG. 1.—DAHLIA FLORETS (ENLARGED TEN DIAMETERS), SHOWING DEVELOPMENT OF THE STIGMAS.

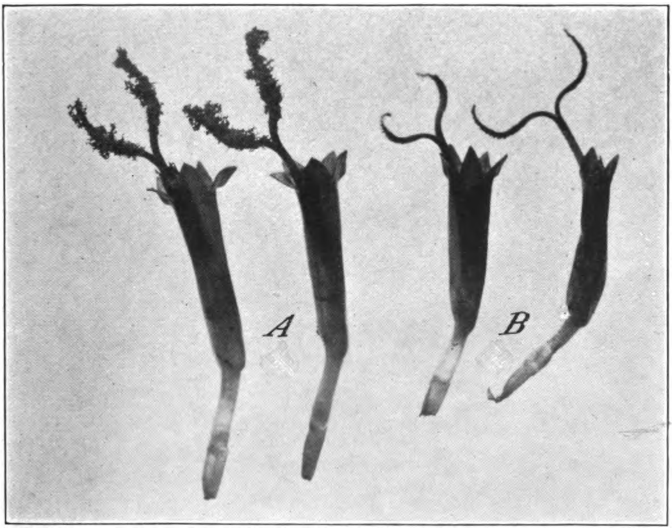


FIG. 2.—DAHLIA FLORETS (ENLARGED SIX DIAMETERS), BEFORE AND AFTER DEPOLLINATION.

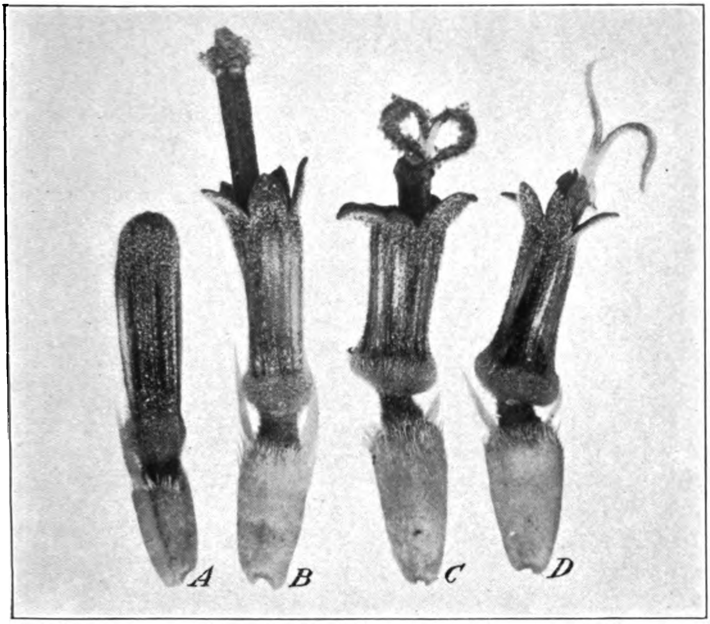


FIG. 1.—DISK FLORETS OF HELIANTHUS (ENLARGED FIVE DIAMETERS), SHOWING DIFFERENT STAGES OF DEVELOPMENT.

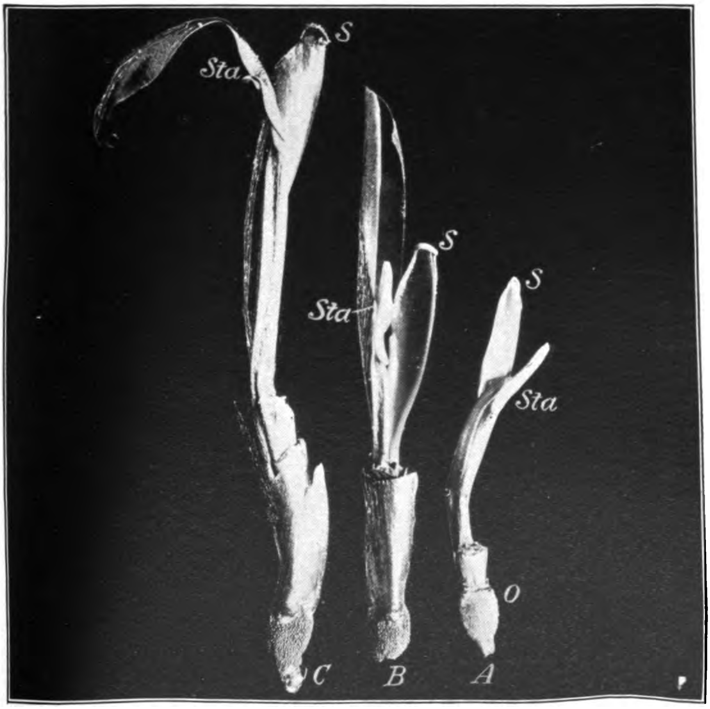


FIG. 2.—FLOWERS OF CANNA INDICA (NATURAL SIZE), SHOWING STAMEN AND PISTIL IN DIFFERENT STAGES OF DEVELOPMENT.

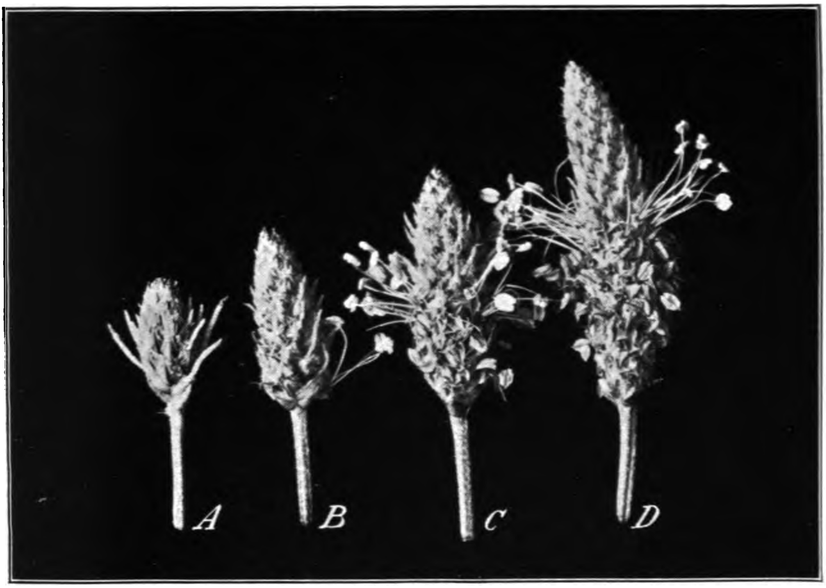


FIG. 1.—FLOWERS (PROTEROGYNOUS) OF PLANTAGO LANCEOLATA, SHOWING PISTILS MATURING BEFORE THE STAMENS.

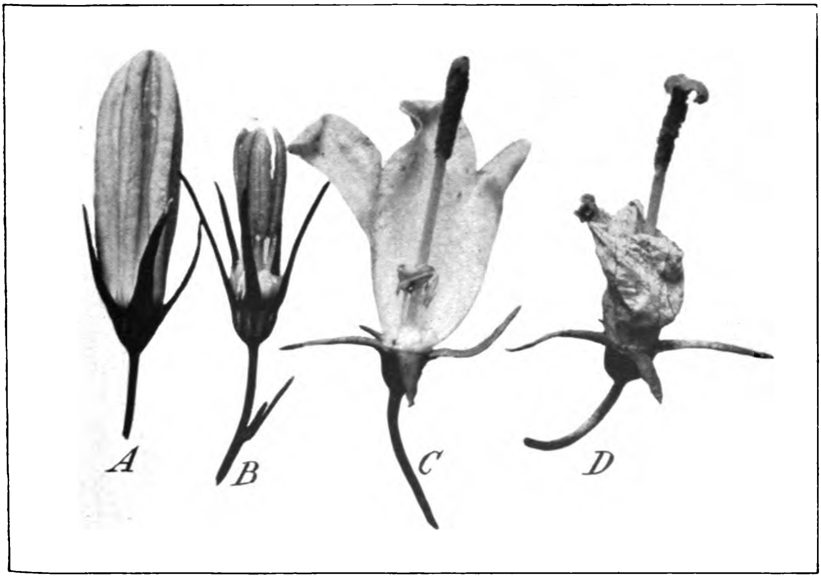


FIG. 2.—FLOWER (PROTERANDROUS) OF CAMPANULA ROTUNDIFOLIA (ENLARGED THREE DIAMETERS), SHOWING THE STAMENS MATURING BEFORE THE PISTIL.

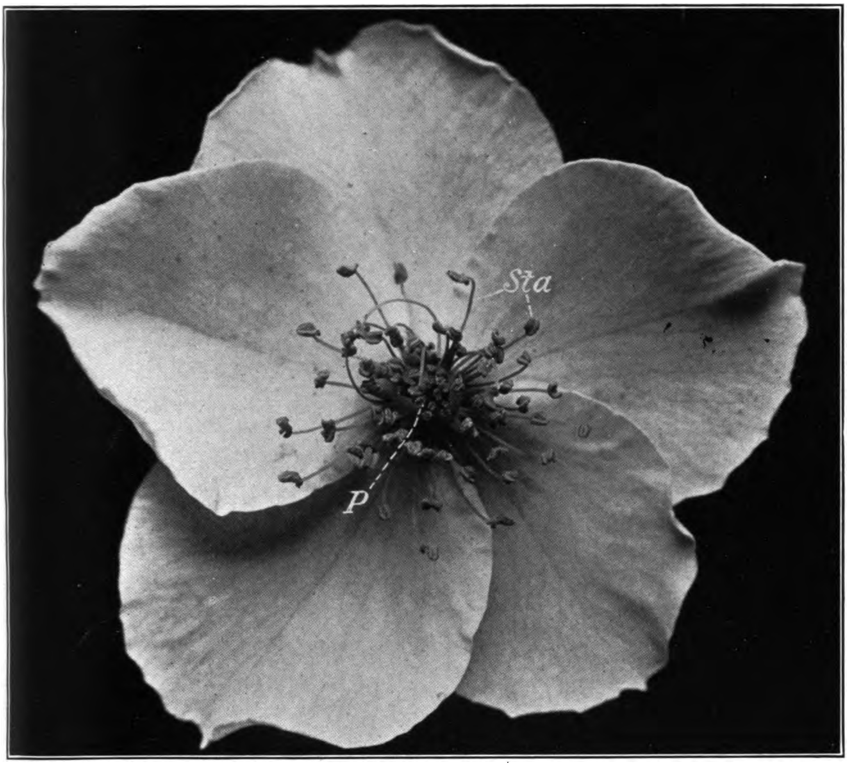


FIG. 1.—SINGLE TEA ROSE, SHOWING HOW EASILY HERMAPHRODITE FLOWERS HAVING LARGE STAMENS MAY BE EMASCULATED.

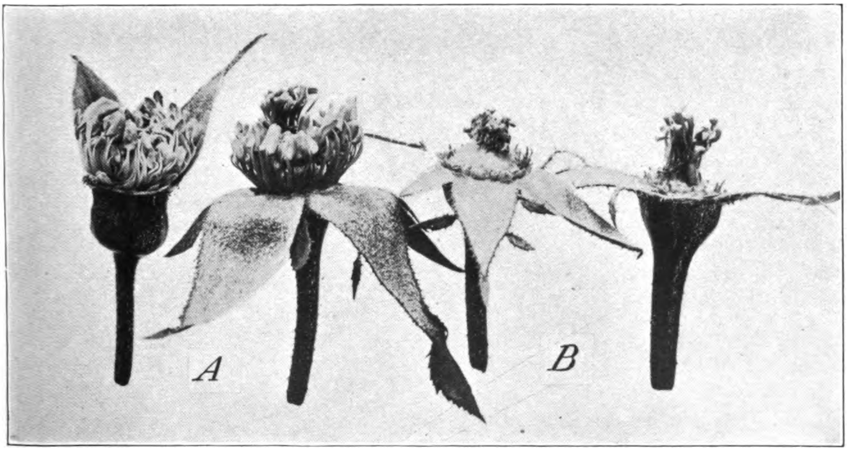


FIG. 2.—FLOWERS OF ROSES (NATURAL SIZE), SHOWING METHOD OF EMASCULATION.

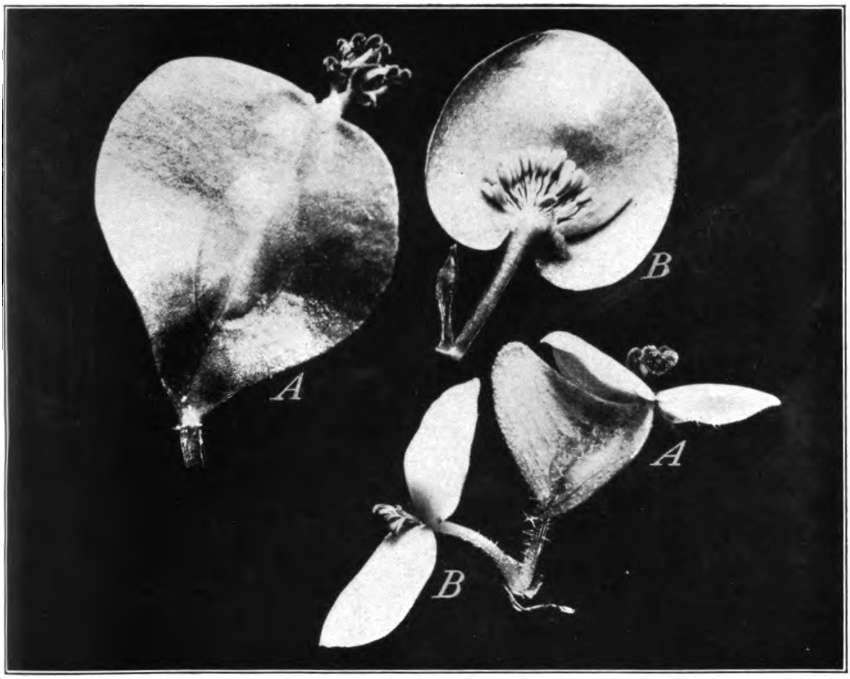


FIG. 1.—FLOWERS (MONŒCIOUS) OF THE BEGONIA, SHOWING THE SEXES IN DIFFERENT FLOWERS ON THE SAME PLANT.

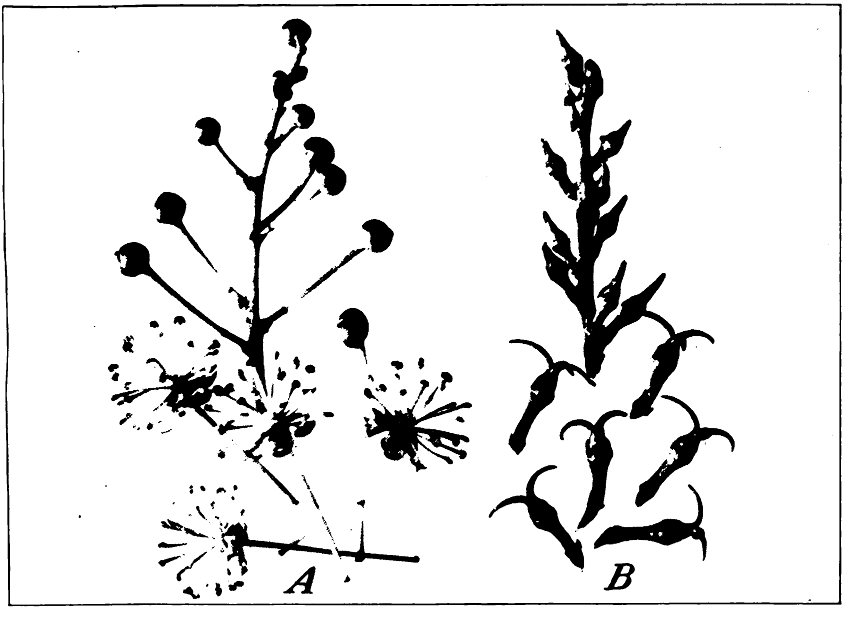


FIG. 2.—STAMINATE AND PISTILLATE FLOWERS OF CODIAEUM VARIEGATUM FROM THE SAME PLANT.

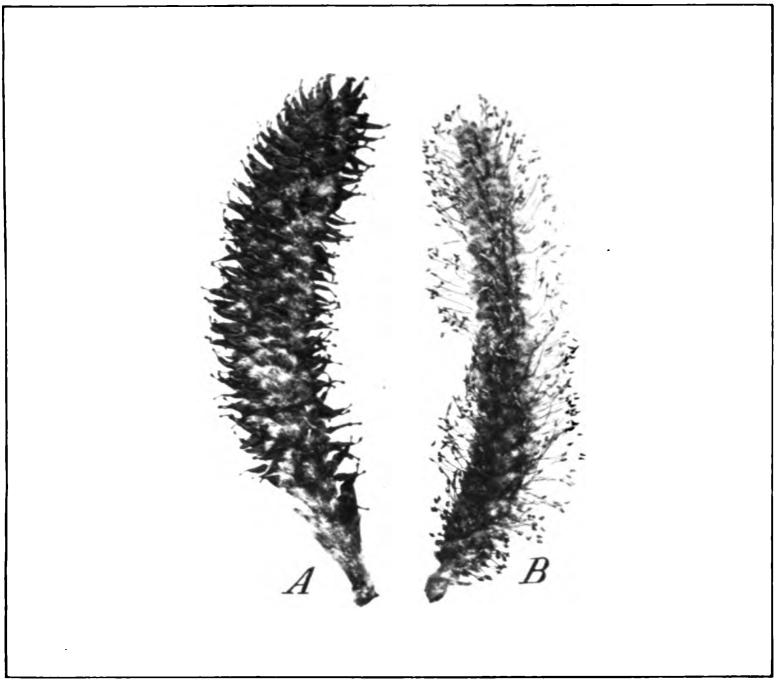


FIG. 1.—STAMINATE AND PISTILLATE (DIŒCIOUS) FLOWERS OF WILLOW, FROM DIFFERENT PLANTS.

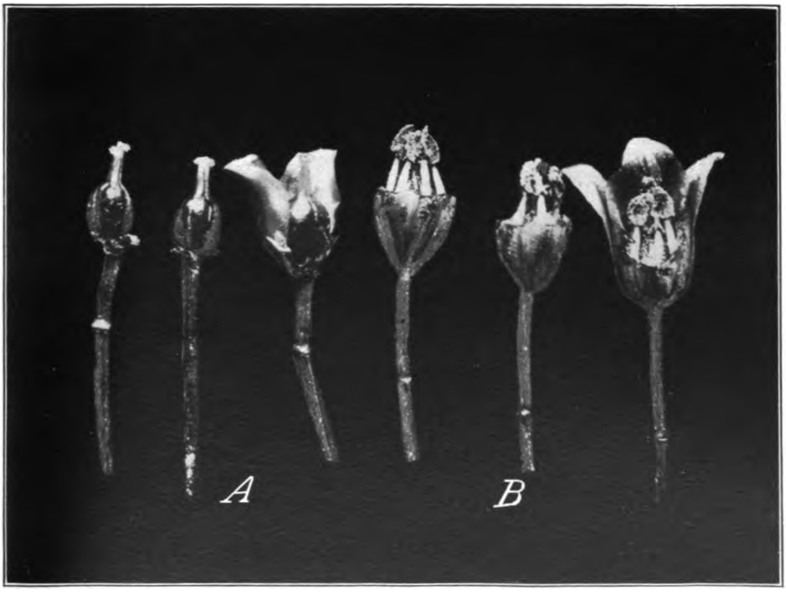
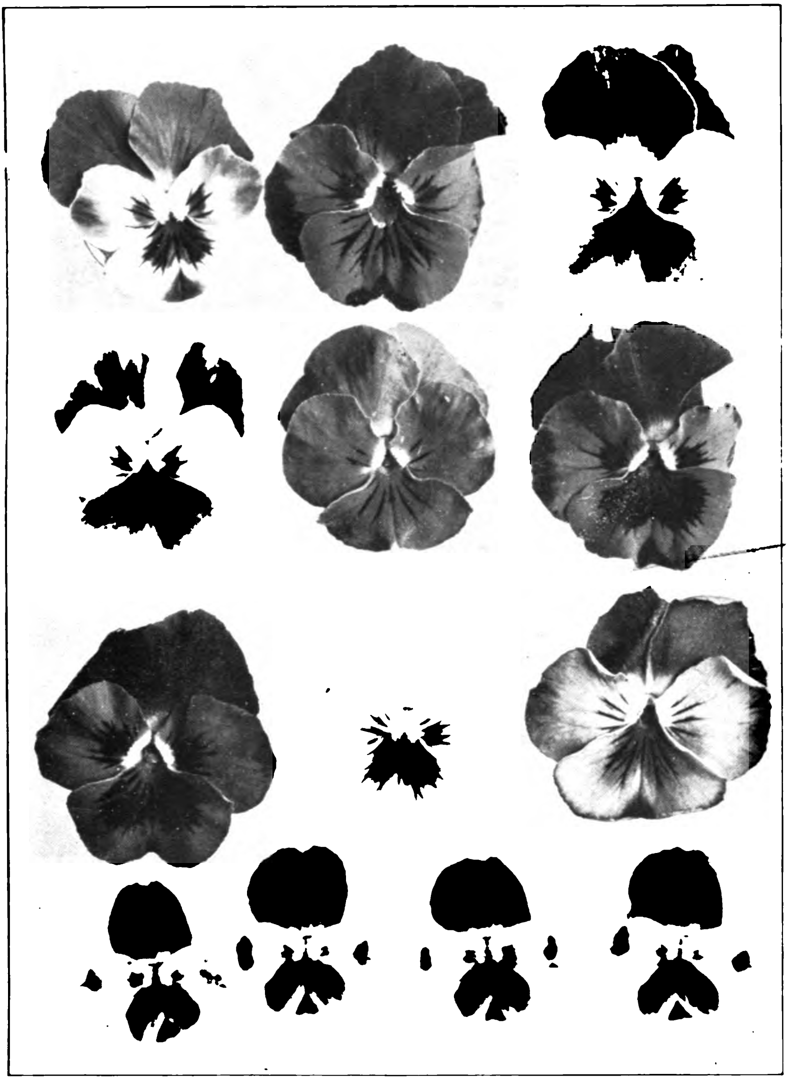
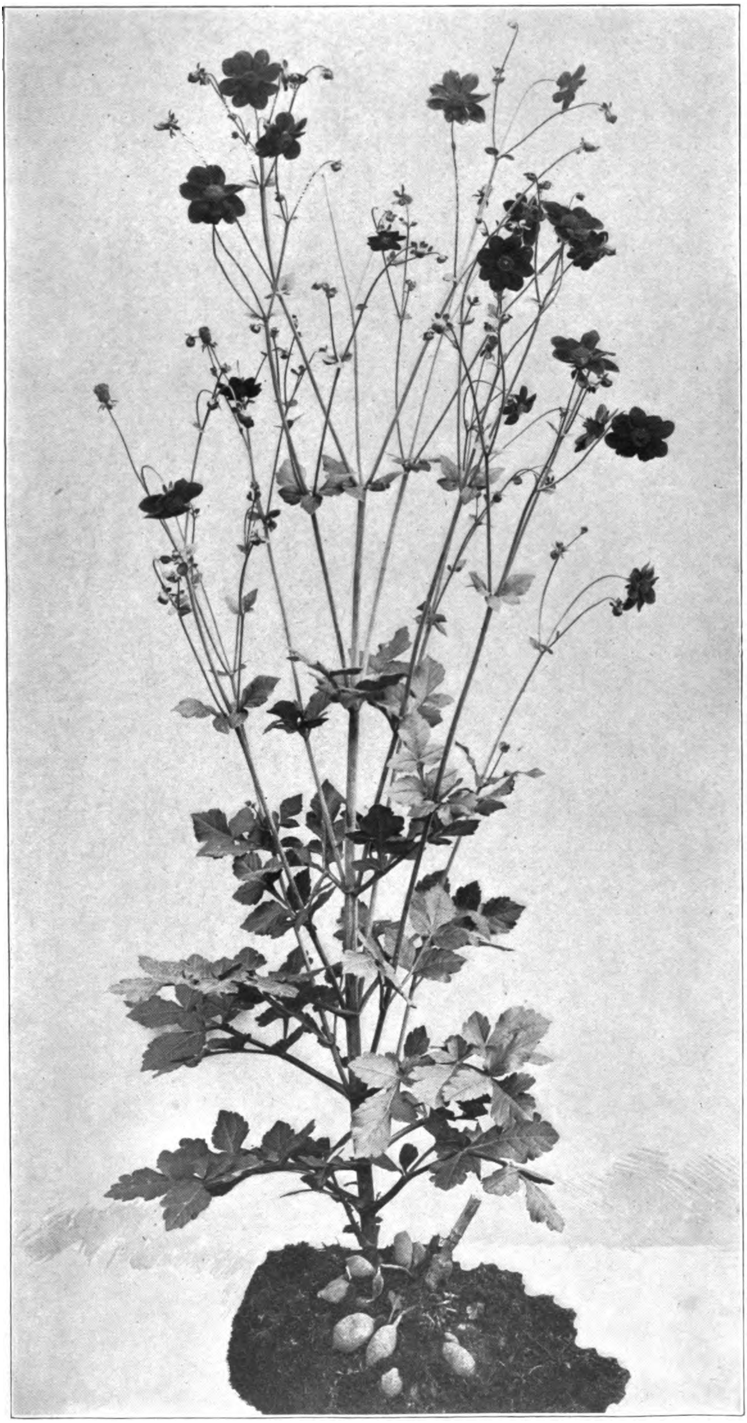


FIG. 2.—FLOWERS FROM STAMINATE AND PISTILLATE PLANTS OF ASPARAGUS OFFICINALIS (ENLARGED FIVE DIAMETERS).



FLOWERS FROM FIRST-GENERATION SEEDLINGS OF CROSSES OF PANSIES (NATURAL SIZE).

Viola tricolor ♀ × cultivated forms ♂. The row of flowers at the bottom is *Viola tricolor* uncultivated.



SINGLE BRANCH OF HYBRID DAHLIA PLANT.

Dahlia chisolmii ♀ × Twentieth Century dahlia ♂.

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